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Mothers and Offspring:
Social Relationships and Social Behaviour of the Kasekela Community of Chimpanzees, at Gombe National Park, Tanzania.

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Abstract

This thesis uses mainly an 18-month dataset, taken from 2001-2003, on the Kasekela community of chimpanzees from Gombe National Park. It explores variation in maternal social behaviour, determines how it influences the social behaviour of dependent offspring and seeks to define chimpanzee play behaviour in terms of both its structure and function. Results show that mothers have well-defined relationships ordered into a female dominance hierarchy. While the strongest social bond is between a mother and her adult daughter, association and grooming patterns reflecting kin, rank and sex preferences suggest that similarly ranked and established females prefer to associate together, as a consequence of contest competition or as an adaptive strategy for effective coalition formation. Furthermore, feeding efficiency and diet quality may determine certain aspects of sociability and female reproductive success. Chapter three shows that diet quality of both mother and dependent offspring determines the social play activity of the latter. Results support the notion of a reduction in play frequency in response to a decline in resource availability and demonstrate that a mother's own association patterns and degree of sociability determines the social milieu of her offspring, whose social network mirrors her own. Chapter four shows that play behaviour is goal-directed and competitive and commonly occurs between ill matched partners. Results support the "social cohesion" and "complex social skills" functional hypotheses of play behaviour. In addition, increasing rates of aggression in play, with age, suggest that as with human adolescents, chimpanzees can use the play context in which to assert dominance and establish dominance relations with other dependent offspring. All functions proposed are viewed as having both immediate and cumulative benefits.

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Author's Declaration

I declare that the work in this dissertation was carried out in accordance with the Regulations of the University of Bristol. The work is original, except where indicated by special reference in the text, and no part of the dissertation has been submitted for any other academic award. Any views expressed in the dissertation are those of the author.

SIGNED.....Elizabeth Greengrass.....*DATE*..May 26, 2005

Table of Contents

1. Introduction

1.1 Aggression & Play

1.1.1 Aggression, Dominance and Sexual Selection Theory

Social group living incurs costs in terms of competition for resources available in the environment. Agonistic behaviour is the pattern of aggressive behaviours by which members of the same species adjust to conflicts arising from competition for the same limited resource (Krebs & Davis 1981). To avoid the detrimental effects of overt aggression, individuals have evolved ritualised aggressive interactions in the form of threats or displays, which convey information about the relative strengths, and weaknesses of the participants, resulting in one submitting to the other before serious injury is inflicted. The winner in effect establishes dominance over the loser and gains access to the resource. Among social vertebrates, ritualised combat of this type, occurring fairly frequently, can lead to the establishment of a dominance hierarchy. Hierarchies are often stable, linear and transitive in nature; that is individual A dominates all other group members, individual B dominates all other group members except A and individual C dominates all other group members except individuals A and B etc.

Following sexual selection theory, the resources over which males and females compete, limiting the reproductive success of each, and the strategies used to increase reproductive success, will differ. As a result, sex differences in competition and aggression will ensue. This follows from the disparity between males and females in the effort put into rearing

an individual offspring from the parent's limited pool of resources (Trivers 1972), differences in parental investment. Females invest heavily into each egg produced and as a result they produce relatively few within their lifetime. A female's capacity to produce eggs is limited by the availability of food resources. The relatively small male gametes, sperm, which are in contrast relatively cheap to produce, are produced in large quantity. Because males can potentially fertilise eggs at a faster rate than they are produced, a male can optimise his reproductive potential by mating with as many females as possible. Females are therefore a scarce resource and males are under strong selection pressure to compete over females.

While parental care increases the likelihood for offspring to survive, it also reduces the number of offspring that can be produced and increases the energy input of the parent involved. Because females initially invest more than males into each offspring, they have more to lose if their offspring fail to survive. Male parental care is less common because the investment is less likely to increase a male's reproductive success if it means time away from accessing fertile females and investing in progeny whose paternity can't be ascertained. Maternal provision of food is thus crucial to the survival of developing offspring. This disparity in parental investment and the higher cost of reproduction for females leads to male competitiveness and female choosiness. If some males have better genes, improving the chances to survive and reproduce, a female can improve her offspring's chances by choosing the fittest male. Dominance encounters and physical aggression between males not only provides information between participants on who

gains access to a resource, but a male's success is an important indicator to the female of male fitness (Dorit, Walker & Barnes 1991).

Sexual competition between males is most acute when there is a shortage of females and in polygynous (as opposed to monogamous) mating systems where there is a greater variation in males', relative to females', reproductive success. Differences in ornamentation, size or sexual dimorphism are greatest in polygynous species where a male's success may depend upon his dominance over other males and his ability to attract mates. Large body size, advantageous in competing for and monopolising females, is believed to have evolved through sexual selection. Competition among males tends to be intense although episodic due to the short-term nature of the limiting resource (Smuts 1987). Since a single food item has a much smaller effect on a female's reproductive success compared to access to a mate for males (Smuts 1987), competition among females tends to be low key and chronic. Since fighting among females could potentially affect their ability to care for their offspring, females use less overt strategies to secure resources.

1.1.2 Play: Intelligence, Function, Costs and Benefits

Play behaviour is present in a variety of species considered intelligent: mammals, birds and even some reptiles such as turtles that have brain structures homologous to mammalian brain structures (Burghardt 1998). Some studies have suggested a link between social complexity and the diversity or presence of social play (e.g. Watson 1998). Other studies have shown that complex social play is associated with absolute or

relative brain size and a lengthy maturation phase in birds (Joffe 1997, Pellis & Iwanuik 2000; in Diamond & Bond 2003) in addition to a persisting association between conspecifics and post-fledgling juveniles in birds (Diamond & Bond 2003). Long periods of immaturity may allow for more learned behaviour that allows for a flexible response in a complex and changing environment. The largest passerine bird, the raven *Corvus covax,* known for its playful temperament, probably has the largest brain volume of any corvid and inhabits the largest geographical range and the most diverse habitat (Heinrich & Smolker 1998).

There is no universal definition of play, although the sequences of behaviours termed as play are universally recognised. Most observers would agree that play is both difficult to define and easy to recognise (Cheney 1978). Play is generally thought to have a vital role in behavioural development but most functions of play predict benefits occur later in life (Burghardt 1998) due to a lack of obvious and immediate benefits. Yet benefits would have greater selective advantage if they acted earlier rather than later in ontogeny because of the cumulative effects of mortality (Martin & Caro 1985) and the fact that natural selection operates at all stages in the life cycle (Gomendio 1988). Play is generally thought to provide juveniles the opportunity to learn, practice or refine a range of social and motor skills, or cognitive skills supporting motor performance, related to intraspecific fighting, prey capture and escaping predation (e.g. Owens 1975a, Byers 1977, Martin & Caro 1985, Caro 1995, Negro et al. 1996, Thompson 1996, Biben 1998, Byers 1998, Hall 1998, Heinrich & Smolker 1998), which are thought to be vital for adult life in a complex environment. In particular, sex differences in play and partner

preferences of participants, suggest that play serves to improve future adult motor skills in a number of species (e.g. Berger 1980, Caro 1988, Byers 1998, and Watson & Croft 1993) although there is little solid evidence to support this (see Martin & Caro 1985). Byers & Walker (1995) take the hypothesis one step further by proposing that play may not be motor-training in the broad sense but a behaviour designed to influence specific types of development that occur at the same time at which play is most marked (during the juvenile period) that influences motor performance.

Play is often categorized as object play: the manipulation of inanimate things, locomotor play: energetic running and rotational body movements and social play: play between two or more individuals responding to each other's actions (Fagen 1981; Thompson 1998). One of the problems in finding a universal and functional definition of play, is that although the superficial structure of play fighting looks similar across species, it's structure in some species does not have the design features suitable for the proposed function (Pellis & Pellis 1998). Such differences imply that play may have evolved (from a common ancestral form) to be multi-functional in nature across species, despite behavioural and superficial similarities. Since species live in a variety of social and physical environments, the kinds of skills they must learn or practice may be very different and play may have evolved to serve different functions specific to different species, for each sex and for different stages in ontogeny. Among species of non-human primates, it is generally believed that play improves the ability of males to fight and assess the fighting capabilities of others, therefore influencing their adult ranks (e.g. Owens 1975a, Cheney 1978) while bearing little influence on the acquisition of rank

among females, who generally acquire ranks similar to their mothers. The function of primate female-infant play is often explained in terms of enabling females the opportunity to interact regularly with infants before they reach reproductive age (Cheney 1978) providing invaluable social or maternal experience. Therefore the failure to identify any function of play may lie in the fact that there is no single function and benefits may be multiple, varying at different points in the life cycle. Indeed, even if one benefit is that for which the behaviour was originally selected (its function) in evolutionary time, other initially incidental benefits may come to be selected for as species have diverged and become more specialised and these may in turn change the form of the behaviour (Humphreys and Smith 1984). Results from some studies support the view that play is a heterogeneous category of behaviour containing several distinct types of play, each with their own controlling factors (e.g. Smith 1991), with separate motivations, different developmental courses and possibly even different evolutionary origins.

Several authors have investigated the direct and indirect costs of play in terms of time, energy and survivorship (e.g. Caro 1986, Harcourt 1991, and Caro 1995). Biologists assume that an animal will only perform an action for which the reproductive costs do not on average exceed the reproductive benefits of its execution (Harcourt 1991); if behaviour has high costs it is assumed to also have high benefits. Similarly if play has low overall costs play need only have small benefits to be favoured. Assessment of the magnitude of costs allows knowledge of something about the benefits to be inferred. While some studies of play have assumed associated high costs confer major benefits, the

assessment of potential costs has often been incomplete (e.g. Martin 1984) and sometimes contradictory (e.g. cheetah cubs *Acinonyx jubatus,* Caro 1986; 1995), while the costs associated with play are clearly large in some species (e.g., South American fur seals *Arctocephalus australis,* Harcourt 1991; and to a lesser extent, Siberian ibex *Capra ibex sibirica,* Byers 1977). The view that if play is not a costly activity, any benefits derived from play may be minimal (Martin & Caro 1985) may be purely speculative. Copulation is an example of a behaviour that probably does not take up a lot of energy but may have large reproductive gains if conception is achieved. It is furthermore, difficult to assess the extent to which the amount of energy expended during play represents a significant cost in the lifetime of the individual (Siviy & Atrens 1992). Siviy & Atrens (1992) showed that while 80% of energy expenditure in the rat is spent on involuntary costs, the 5% total energy expended in play makes up a significant proportion of the remaining 20% devoted to voluntary activity. It is the difficulties in demonstrating the adaptive significance of play that have resulted in the proposition of a "purposeless" neutral function that is able to survive as a by-product of selection for some other trait, persisting, at least for a while, because although it doesn't contribute to the individual's fitness neither does it detract from it (Chism 1991). However such a view presents a paradox for biologists who assume that behaviour is performed only if there are benefits, which outweigh the costs.

1.1.3 Play and Aggression

The similarity between play fighting and real fighting has led to the generally accepted theory that play fighting allows the young of a species to practice and rehearse adult

behaviours related to intra-group aggression that benefit the individual in terms of reproduction and survival as an adult, within a safe environment. Play is viewed as a specific developmental determinant of adult behaviour and is often defined in terms of non-serious fighting lacking the obvious consequences (Martin & Caro 1985) apparent in fighting. Supporting this theory are studies on human children showing that while young children's rough-and-tumble-play (R&T) rarely results in aggression, during adolescence the two increasingly co-occur together (e.g. Humphreys & Smith 1984). Furthermore, males more than females engage in R&T and this difference has been observed in most nonhuman primate species (Pelligrini 1995). These observations support the notion that play may function as practice for adult aggression. In some species however, aggressive behaviours emerge prior to playful ones suggesting that play is not necessary for the emergence of agonistic behaviours (e.g. olive baboon *Papio anubis*, Owens 1975b; spotted hyenas *Crocuta crocuta* Drea, Hawk & Glickman 1996). Furthermore, a few studies have shown fundamental differences in the structure of real fighting versus play fighting; the specific body parts targeted in attack and defence are different (e.g. Pellis 1993 in Thompson 1998) and certain potentially injurious manoeuvres crucial for the successful performance of real fighting are missing in play fighting (Pellis & Pellis 1998).

1.2 Competition and Sociability among Female Primates

1.2.1 Machiavellian Intelligence

Chimpanzees *Pan troglodytes,* live in closed groups called communities where members recognise and interact with one another as individuals over the course of relatively long lifetimes in such a way that earlier interactions influence later ones (Cord 1997). Whenever two individuals meet, their behavioural interactions may have consequences that will influence all of their subsequent interactions (Pusey & Packer 1998). Primates distinguish kin from non-kin, act differentially towards conspecifics of differing dominance ranks and discriminate among their own and others' close associates. They appear outstanding compared to other species in their ability to maintain simultaneously many different kinds of relationships (Essock-Vitale & Seyfarth 1987). In this sense, each member forms a network of social relationships and each relationship has a unique and potentially long history (Cord 1997). Social relationships ultimately function to maintain group cohesion, integration and peaceful coexistence between dominant and subordinate animals, where group living is individually beneficial in solving ecological problems. By living in groups, companions may benefit from reduced predation risk, improved defence of resources or communal rearing but they may also suffer from increased competition over critical resources (Pusey & Packer 1998). On a day-to-day basis, social relationships, mutual investments, serve social attraction and resolve social problems within the group, such as intra-group competition for food or mates. Jolly (1966) identified that the social complexity within primate groups may have been the key

selective force acting on primate intelligence to evolve cognitive skills that reflect both coercion and compromise, such as deception, cooperation and social manipulation. Whiten & Byrne (1988; in Whiten & Byrne 1997) termed this Machiavellian intelligence, a political intelligence that allowed the actor to choose alternative tactics or strategies creatively to a range of social problems; the decision-making capacity enabling social animals to further their self-interest in situations involving rivalry and questions of power and leadership (Boehm 1997). Under this view, primate social life is seen as complex because individuals have to closely monitor, make predictions and respond innovatively and flexibly under specific social rules, to each other. They must cognitively assess each social situation and coordinate their actions. The highly structured group life of most primate species did not evolve through the disappearance of competitive and aggressive tendencies but through the development of powerful mechanisms of conflict resolution (de Waal 1987), such as reconciliation and tolerance. Chimpanzee societies are particularly complex because the constant fissioning and fusing of subgroups means that outcomes of dominance interactions and the likelihood of aggressive and affiliative behaviour depends upon which individuals are in a party (Williams, Liu & Pusey 2002) at any one time.

1.2.2 Ecological Model of Female Bonding

Wrangham (1980) developed an ecological model to explain the evolution of female social relationships and why most primate groups are based on a core of resident and closely related females. The model explained the adaptive significance of female bonded relationships in terms of female foraging strategies, which are largely determined by

ecological conditions. Since the behavioural strategies of males (to increase access to fertile females) are determined primarily by the behaviour and distribution of females (Mitchell, Boinski & van Schaik 1991), female strategies are thought to ultimately shape the social system. Wrangham (1980) suggested that female co-operation between closely related kin evolved as a way to defend key food resources against females in other groups, and the benefits of this outweighed the costs of intra-group competition. Van Schaik (1989) expanded the model, proposing that both between and within group competition influenced female social relationships; he emphasised predation risk as a major determinant of grouping that created ideal conditions for intra-group competition. Female social relationships and the degree of female relatedness therefore reflected competition among females for food and safety (van Schaik 1989). This view gained support from comparative studies, e.g. Mitchell, Boinski & van Schaik (1991) and Barton, Byrne & Whiten (1996), which found that where food patches were monopolizable females formed linear hierarchies, where there was little or no inter-group competition. Isbell (1991), in contrast, supported Wrangham's model, arguing that both food abundance and distribution were sufficient to determine female relationships between groups and within groups, respectively. Sterck, Watts & van Schaik (1997) proposed that it was contest competition between and within groups that largely determined social relationships between females.

1.2.3 Competition and Female Dominance Hierarchies in Primate Groups

Contest competition occurs in situations where there is high spatial variation in the quality of the food source and food patches are defensible. Some individuals can

increase their net food intake by monopolising access to it. In these situations wins and loses can have far-reaching effects on female reproduction. Dominance hierarchies, reflecting the social partitioning of resources (Barton & Whiten 1993), evolve that are consistent, commonly transitive and linear, despotic and nepotistic. Affiliative and supportive relationships among female kin form when they raise the inclusive fitness of the individuals involved. Frugivorous and omnivorous species generally form despotic and nepotistic ranking systems accompanied by female residence. Dominance relationships are clearly defined and usually linear and female relatives rank close together.

Where food crops are dispersed and indefensible, scramble competition prevails. The net food uptake of all individuals is equally affected by an increase in the population's density. As group density increases, all members suffer an equal reduction in efficiency (van Schaik 1989) and no individuals can obtain more through overt and aggressive behaviour. As groups increase in size, food patches are depleted more quickly, and larger groups may have to travel further per day than smaller groups in order to consume the same amount per individual (e.g. Clutton-Brock & Harvey 1977). In this situation dominance hierarchies are of little value to group members and as a consequence, support among female kin and the formation of aggressive coalitions rarely occurs. Folivorous species of primates generally experience scramble competition and as a result, form egalitarian and individualistic ranking systems where female bonding varies. Dominance relationships are poorly defined and the ranks of female relatives tend to be independent of each other (Sterck, Watts & van Schaik 1997).

1.2.4 Feeding Competition, Dominance and Dispersal Patterns among Female Chimpanzees

Chimpanzees are unusual among primates in their preference for ripe fruits. Rather than switching to an alternative "subsistence diet" during periods of food scarcity (Wrangham 1980), as is the case for other primates, leading to reduced feeding competition, chimpanzees are restricted to small high quality fruit patches (see also Wrangham, Conklin-Brittain & Hunt 1998). To reduce feeding competition community members forage in smaller parties or alone e.g. Chapman, Wrangham & Chapman (1995). The fission-fusion nature of chimpanzee society therefore allows a flexible response to food availability and predation pressure (Boesch & Boesch-Achermann 2000). Their large body size and semi-terrestrial nature frees them from the costs of group cohesiveness, resulting from a high predation risk and allows them a flexible response to the food supply so that competition falls below the level of net food intake (Sterck, Watts & van Schaik 1997). This has been the traditional explanation for why females do not co-operate, the nature of their diet forces females to forage alone and avoid other females. Historically therefore, intra-group competition for resources was not thought to occur, or at the best was limited and female relationships were thought to be both undifferentiated and unimportant (Wrangham 1980) because female chimpanzees avoided each other. However, there is growing evidence that intra-group competition is extremely important to female chimpanzees in some populations at least. High-ranking females, who clearly dominate other females, have been known at a number of field and captive sites (e.g. de Waal 1982; Goodall 1986; Nishida 1990, in Pusey, Williams & Goodall 1997; and Boesch & Boesch-Achermann 2000). Hierarchies, if present however, were considered ill

defined. Dominance interactions were rare, not always clear-cut in terms of a winner and loser and were never observed between some dyads.

Female social relationships will reflect the strategies for obtaining increased reproductive success (Wrangham 1980) and there is growing evidence of variance among chimpanzee female strategies from different populations. Goodall (1986) found that 33% of observed aggression by adult females at Gombe was directed to other females compared to 0% at Kanyawara in Uganda (Muller 2002). Although parous females frequently pant-grunted to adult males, they were rarely observed to pant-grunt to other parous females (Muller 2002). At Budongo, also in Uganda, no females were ever observed to pant-grunt to other parous females (Emery, personal communication) within one 14-month study. These results suggest that female chimpanzees at Gombe have a better-defined hierarchy than at other field sites. Confirmation of a hierarchy came from Pusey, Williams & Goodall (1997) who assessed dominance relationships among the female chimpanzees at Gombe, by examining the direction of all pant-grunts, the most reliable measure of submission (de Waal 1982), from 35 years of long-term data. They showed that dominance rank influenced three measures of reproductive success: higher infant survival, faster maturing daughters and more rapid production of young.

The ultimate benefit of dispersal is inbreeding avoidance. In terms of dispersal patterns the chimpanzee is just one of six primate species (bonobo *Pan paniscus*, spider monkey *Ateles species*, red colobus *Colobus badius* and hamadryas baboon *Papio hamadryas*) where males remain in the community/group in which they were born and females

disperse at sexual maturity and transfer into a new community. Van Schaik (1989) predicted that where females no longer form cohesive groups and are more dispersed, the optimum male strategy is most likely to shift from female defence polygyny to resource defence polygyny (van Schaik 1989) and hence the establishment of territories. Since the successful defence of a territory containing any number of dispersed females requires co-operation between a group of males, these males are likely to be relatives, since effective co-operation requires permanent and established bonds. Such a shift provides strong selective pressure for female dispersal.

Because of male philopatry chimpanzees are termed male-bonded, since males are more closely related than the females in a community. At Gombe, females range in small overlapping core areas, clustered into a north and south neighbourhood (Williams *et al.* 2002). Most females show a high degree of site fidelity but alter their space use patterns to stay within a male defended boundary (Williams *et al.* 2002). Along with the fact that males can be intensely aggressive towards stranger females encountered outside the community boundary, these observations support the male bonded model of chimpanzee social system, where male coercion forces females to be members of one community, exclusively. As predicted by van Schaik (1989), males defend the community resources (Williams *et al.* 2004) and attempt to expand the community range. Range expansion has benefits for females (increased body weight and reproductive success) but may also be a male strategy to increase access to females, since as a consequence, females spend more time in mixed groups and males encounter females more often (Williams *et al.* 2004). Female chimpanzees are freed from the task of resource defence and exert little influence

over group decisions. This could be a proximate reason for why females are the dispersing sex. While male strategies may be a result of female distribution, as in many primate species, male chimpanzees appear ultimately able to control female distribution by controlling females' access to food resources.

Contradicting this general picture of male philopatry and female dispersal, Pusey, Williams & Goodall (1997) calculated that about 50% of all females at Gombe do not disperse at sexual maturity but remain in their natal community as adults. The degree to which females disperse and transfer will affect group composition and relatedness among group members (Sterck 1997). The commonality of mother and adult daughter pairs, observed at Gombe, is an unusual consequence of the high degree of female philopatry. Female residence is often, but not invariably, related to despotic systems and their variants (Wrangham 1980). These significant rank effects on some aspects of offspring production and "untraditional" dispersal patterns found at Gombe do not therefore support the traditional view of female chimpanzees.

Williams *et al.* (2002) also found that relationships were highly differentiated among female chimpanzees at Gombe. High-ranking females associated most together, then with middle-ranking females and least with low-ranking females. Low-ranking females showed the reciprocal of this relationship. Established females, showing high site fidelity to one of two neighbourhoods, associated most together and least with new immigrants. New immigrants showed intermediate association patterns. These results suggest that

contest competition is an important aspect of female associations at Gombe (Williams *et al.* 2002).

1.2.5 Primate Sociability and Grooming

Grooming is considered a good index of affiliative relations among female primates and the study of the factors affecting the distribution of grooming within a social group can illuminate the principles governing primate social structure (Schino 2001). No attempt to describe primate sociality or to determine its organizational principles can succeed without an understanding of how and why grooming is deployed in the service of reproductive success (Henzi *et al.* 2003). Grooming should be sensitive to changes in resource competition; for example, in situations where between-group competition is more important than within-group competition, we expect, accompanying weak dominance relationships, reciprocal grooming relationships that promote cohesion among group members (Payne, Lawes & Henzi 2003). Where within group competition is high, and despotic dominance hierarchies emerge, grooming should be directed to higher-ranking animals in exchange for tolerance in feeding competition (Dunbar & Dunbar 1992).

Seyfarth (1977) proposed a model to explain the distribution of grooming among female primates in terms of an attraction to high ranking individuals (because of their value as coalition partners), an attraction to kin and an interaction between these idealized grooming objectives of females and competition for valuable grooming partners (Heinzi *et al.* 2003). An analysis of grooming behaviour in 27 different social groups belonging

to 14 different primate species by Schino (2001) confirmed the majority of Seyfarth's predictions although some studies run contrary (e.g. Parr *et al.* 1997).

1.3 Maternal Influence on Sociability of Primate Offspring

1.3.1 Maternal Influence on Development

Maternal behaviour is critical for infant survival in mammals, and for this reason we can assume it has been subject to intense selection through evolutionary history (Nicolson 1991). The ways in which primate mothers influence the development of their offspring, notably infants, has been well documented. Primate mothers produce relatively few young and have relatively long inter-birth intervals, while immatures experience a long period of dependency, suggesting that parental investment in offspring is high. Infant contact is of particular importance since primate mothers do not leave their offspring in nests. The importance of the mother in alleviating stress (Maki, Fritz & England 1993) and providing a secure base supporting the exploration of novel stimuli, a prerequisite to behavioural adaptation and development (Miller *et al.* 1986), has long been recognised. The mother as the main caregiver provides psychological comfort, a base from which to explore, nutrition, transportation and protection from both predators and conspecifics and extremes in weather conditions. Rearing experiments by Harlow (see Nicolson 1991 for a review) demonstrated that captive rhesus infants reared without a mother developed extremely inappropriately in comparison to those reared with a mother, with females showing gross deficits in maternal behaviour towards their first-born infants.

All primate infants are nutritionally dependent upon their mothers for the first few months of life, and for some primates, infants continue to suckle at a reduced frequency for several years after that (e.g. all Great Ape species). Lactation is an energetically expensive form of parental investment, increasing the current offspring's chance of survival and decreasing the parent's ability to produce and care for future offspring (Nicolson 1987). Altmann (2001), modelling the energetic demands of both yellow baboon *Papio ceynocephalus* mothers and their infants, demonstrated that a mother could not provide all caloric requirements for herself and her infant beyond six to eight months of life and probably could only do so up to that age with difficulty and major restructuring of other aspects of her life (Altmann 2001). An infant's maturation and learning and other factors that facilitate the transition to nutritional independence have probably been under considerable selective pressure (Altmann 2001), since weight loss of mothers accompanying prolonged infant nutritional dependence would reduce maternal health, increase susceptibility of death and therefore decrease the chances of offspring survival.

1.3.2 Maternal Influence on Offspring Sociability

The processes by which non-human primate infants develop individual patterns of distributing social interaction among various group members, i.e. social networks, in free-ranging, lineage-based groups are not well understood (Berman 1982). Just what role does a mother play in facilitating her offspring's development into socially competent individuals within a complex social environment, and how does this role interact with the "attractiveness" of the infant to other group members? Hinde & Spencer-Booth (1967)

acknowledged that an infant's relationship with individual peers depended upon the relationship between their respective mothers. However, from an early age infants are socially attracted to other individuals and energetically seek out social interaction with them. Altmann (2001) showed that social factors of the mother, such as a female's dominance rank and the presence of closely related kin and other allies, can influence the maternal style and behaviour she displays, especially how much she restricts or encourages infant independence (Nicolson 1991), that could have far reaching consequences during development and in adult life. Differences in maternal style could be viewed as an adaptive strategy and seen to represent both lifetime and immediate responses of individuals to the pressures of their social world (Altmann 2001). In a wide range of primate species the offspring of high-ranking females receive less aggression and receive more affinitive gestures than the offspring of low-ranking females (e.g. rhesus macaques *Macaca mulatta*, Sade 1972; stumptail macaques *Macaca arctoides*, Gouzoules 1975; pigtail macaques *Macaca nemestrina*, Massey 1977; Japanese macaques *Macaca fuscata*, Kurland 1977; baboons, Cheney 1977, 1978; vervets *Cercopithecus pygerythrus*, Berman 1980, Cheney 1983; in Nishida & Hiraiwa-Hasegawa 1987). In baboons, higher-ranking females primarily instigate supplanting to lower-ranking females and infant pulling and handling, causing visible signs of distress in the mother and probably causing distress to the infant too. Social pressures such as these appear to drive adequate maternal behaviour since a mother's maternal style affects the access of her infant to the social world. Relaxed mothers, who also tend to be high-ranking, produce socially attractive offspring who are groomed more often than the offspring of low-ranking females. Agonistic encounters may be the major factor

determining offspring dominance rank according to maternal dominance rank, providing the opportunity for offspring to learn its mother's social relationships and rank position. Berman (1982) showed that rhesus monkey mothers passed on their social networks to their infants. Infants interacted more with close kin than distant kin or non-relatives and thus functioned as members of their lineage from the beginning (Berman 1982). Berman suggested that the persistence of these patterns in infants as old as 30 weeks, at a time when the responsibility is on the infant to maintain proximity to the mother, demonstrated the long-term consequences of maternal influence on the development of offspring social networks.

As in other social species, young chimpanzees must learn to interact effectively with others (Goodall 1986). Thus, although female chimpanzees may benefit by feeding alone, mothers may benefit by spending time with other chimpanzees in order to socialise their offspring (Williams, Liu & Pusey 2002). For chimpanzees, little is known about how the social characteristics and experiences of a mother and the presence of siblings influence the social development of offspring, although both the mother's rank and the presence and number of siblings has indeed some effect on the development of social behaviour (Yoshida, Noises & Kitahara 1987; Spijkerman *et al.* 1995). Because in many non-human primates, dependent offspring play more frequently with their sibling than other animals of their sibling's age and sex, the availability of siblings will clearly affect the distribution of play partners (Cheney 1978). Brent *et al.* (1997) found that infant chimpanzees with siblings, at Gombe National Park, spent more time socially interacting with their siblings than infants without siblings, who spent more time interacting with

other group members. However, overall levels of social interaction were maintained by both groups (those with and those without siblings), indicating an optimal level of social interaction (Brent *et al.* 1997), which the infant was responsible for seeking out. Furthermore, in chimpanzees, where due to demographic differences social organisation precludes infant peer groups, the sibling may play a definitive role. For chimpanzees, living in fission-fusion societies where party membership is constantly changing, the onl long-term party is a mother with her dependent offspring (Nishida & Hiraiwa-Hasegawa 1987). Consequently, because the mother coordinates travel and controls with whom her dependent offspring are brought into contact with, she may determine and influence the social milieu of her offspring more than mothers of other species who live in permanent social groups. If there are large differences in the social experiences of mothers then these should also translate across to their offspring; if high-ranking females range in nutritionally richer core areas, they may spend a greater proportion of their time in more socially co-operative behaviours, suggesting that high-ranking females may produce more social offspring. While the mother and the presence of other offspring may place an upper limit on the amount of social interaction possible, the level of social interaction within this range may be up to the offspring.

1.4 Chimpanzee Social Play

1.4.1 Functions of Social Play Behaviour

Young chimpanzees show all categories of play and interspecific play occurs most often with juvenile baboons at Gombe. Social play is commonly subdivided into two broad categories: approach-withdraw/chasing and wrestle/rough-and-tumble (Stevenson & Poole 1982), which are both exaggerated and repetitive in nature. Many researchers have described similar patterns in social play in other species and have identified elements such as physical restraint, self-handicapping (e.g. squirrel monkeys, *Saimiri* species, Biben 1998), role reversal, a mixing of behavioural patterns from different motivational contexts, and high levels of reciprocity in a relaxed motivational field that describe certain aspects of chimpanzee social play. Self-handicapping, for example, which infers a degree of intentionality, is most conspicuous when performed by an adult playing with a much smaller immature in many primate species including chimpanzees.

Play is the most frequently observed social behaviour between chimpanzee dependent offspring. Social play may therefore be the very first context in which young are able to socially integrate by forming social networks and learn about social relationships. Ultimately, play could function to establish and maintain cohesion between group members, as seems probable for other species e.g. infant spotted hyenas *Crocuta crocuta,* Drea, Hawk & Glickman (1996). Goodall (1986) considered that chimpanzees, who have long been documented with "political IQ" (e.g. de Waal 1982), learn about power, dominance and submission while young, from observing adults and through social play

where they sharpen their fighting and bluffing skills as they learn to inhibit their aggressive behaviour within the group (Goodall 1986).

Aggression compels attention and youngster watch fights and displays with interest (Goodall 1986). This may underlie the fascination shown by young males in the behaviour of adult males (Goodall 1971). Young chimpanzees learn about aggression during social play; as dependent offspring grow, play becomes rougher and is often terminated because one individual becomes too rough. Through social play a young chimpanzee may learn skills in fighting ability, the ability to form alliances, the strengths and weaknesses of his partners and about his mother's rank in relation to others. Watts & Pusey (1993) found that dependent offspring played with companions of similar age more than they played with older or younger companions, when present and also found sex differences in play behaviour, although sex differences in the social interactions of infants, in another study, were not found (Brent *et al.* 1997). Prutz & Bloomsmith (1996) showed that the age and sex of immatures affected their degree of sociability and Pusey (1990) observed the same variables affecting measures of aggression.

1.5 The Study

1.5.1 Aims of the Study

There are three main aims to this study that focus on the behaviour of mother chimpanzees and their offspring. Having studied the same mother-offspring family groups over a relatively long period, between 1996 and 2003, I have chosen three inter-related topics with the objective to increase overall understanding of maternal and

offspring behaviour in chimpanzees and primates in general. One of the aims is to understand the factors that affect female social relationships and the variance in reproductive success observed between the female chimpanzees at Gombe. The second aim is to understand how a mother's sociability and association patterns affect her offspring's degree of sociability. Since most socialising between dependent offspring occurs within the play context the focus here is on social play behaviour. The final aim of the study is to try and identify any short-term and long-term benefits (functions) of social play.

This is a correlational study, searching for associations between different behaviours by exploiting the natural variation within a population. While results can lend support to both the cause and effect of behavioural phenomena and functional hypotheses, they cannot prove either beyond doubt. Other kinds of study, such as experimental ones, provide more solid evidence, but are impossible (and unethical) to implement in wild populations. While captive studies on chimpanzee play behaviour have been implemented (e.g. Paquette 1994) the differences in the social and physical environment probably have a marked effect on both its form and function. Therefore, in order to gain insight into chimpanzee behaviour and its functional significance, captive studies can only complement studies on natural populations.

1.5.2 Chimpanzees as a Model Species

Chimpanzees are a good model species to help forward knowledge on these topics.

Chimpanzees live in socially complex societies and have evolved multifaceted

mechanisms to deal with competition inherent in group living. Traditionally, most research on chimpanzee social relationships has focused on male relationships, probably because male aggression is more conspicuous (males are more "impressive") and dominance-related behaviours occur more frequently between males than between females. The view that female social relationships are unimportant is less likely to be fact and more likely to be, in part, a consequence of the bias towards studying the "eye-catching" behaviour of males while ignoring the more "subtle" behaviour of females, in some populations at least. Gombe National Park is a particularly good study site to study female social relationships for a number of reasons. First most members of the Kasekela community are well habituated and all community members are known. The Kasekela community has been studied for over 40 years, which means that the life- and family-histories of all members born into the community are also known. The female chimpanzees of this community also appear to differ in a number of ways to female chimpanzees from other sites and populations in that their relationships are established into a relatively defined and stable dominance hierarchy and there is a large variance in reproductive success among females. While some females never produce offspring who survive to reproductive age, one female, at the time of this study, had produced a total of eight surviving offspring, five of which had reached adulthood. Therefore, studying the factors affecting female social relationships and reproductive success, may lead to a greater understanding of inter-population variance.

Gombe National Park has faced increasing pressure from the human population surrounding it and is presently an "island" park isolated from any remaining forest tracts,

which might be habited by chimpanzees. While the differences in female social relationships evident at Gombe and different from those at other study sites may be a product of ecological differences in, e.g. food distribution and availability between sites, other human-induced ecological changes may have had some effect on some aspects of chimpanzees' lives, such as dispersal patterns. At the time of this study one of the three communities was facing extinction due to a dramatic decrease in the number of males and a subsequent influx of females into the Kasekela community. While this study doesn't specifically seek to identify human-induced factors and the extent to which they affect social relationships, understanding female social relationships within this context is important because the differences may, in part, be a product of adaptation to these changes and globally chimpanzees are threatened primarily by habitat degradation and encroachment from human populations. Therefore some behavioural differences such as the heightened degree of female philopatry observed at Gombe may in fact provide good indicators of a population's status and learning just how adaptive chimpanzees are may enable us to predict their ability to survive in disturbed environments.

Chimpanzees are also a good species in which to study social play, notably because it forms a conspicuous and innovative part of their behavioural repertoire, captivating human audiences observing them in the wild or in captivity. Chimpanzees play throughout their lives and social play is the main form of social interaction for dependent offspring; social play must therefore serve some purpose. Gombe is a good study site in which to study social play between dependent offspring because all individuals are known along with their family histories. Understanding social play in terms of partner

preferences, most frequent play partners and social play networks may provide important insights into the adaptive significance of social play. Furthermore, all offspring are well habituated to human observers, providing optimal conditions in which to record in detail the structure of social play interactions, seek out functional explanations, and construct solid definitions. While definitions of play abound, most are unsatisfactory in some way or another due to its probable multi-functional nature across species, which precludes a generalised definition. However behavioural definitions are an important indicator of the extent to which we understand behaviour and are therefore important to create as a product of current understanding.

Finally, the ancestors of the present day *Pan troglodytes* were the last to diverge from our hominid ancestors, 5-8 million years ago. From an evolutionary perspective, chimpanzees are a model species in which to understand early hominid evolution and the origins of our own behaviour. While this study does not condone human violence and aggression (because being present in chimpanzees we assume it has been present continuously in our own evolutionary history) it hopefully illustrates that social behaviours such as aggression, as well as play and affiliative social behaviours, form an important part of our behavioural repertoire. Studying aggression's developmental path in chimpanzees, can only further our understanding of its development and origin throughout our own history.

1.5.3 The Study Site

Gombe National Park in the Kigoma region of Tanzania marks the eastern limit of the chimpanzee's range. Estimated in the region of 35 square kilometres, Gombe comprises

thirteen valleys in a narrow strip of land along the eastern edge of Lake Tanganyika that ascends up to over 1500 meters above sea level to the crest of the rift escarpment. Valleys narrow in the south of the Park, the escarpment is lower and as a probable consequence of wild fires, the vegetation markedly changes, becoming drier in the south.

Gombe is made up of a mosaic of semi-deciduous forest types and grasslands (Collins and McGrew 1988). All valleys have streams and hence evergreen forest traverses watercourses while valley ridges are characterised by open-woodland vegetation and grassland. The year can be divided into a rainy and a dry season. From mid October to mid April there is a good deal of rain while the rest of the year is dry. As a result of the seasonal climate, food availability is extremely patchy both in time and space. Trees and plants that provide food for the chimps are found in the semi-deciduous and evergreen forest and open woodland.

1.5.4 Thesis Structure

In chapter two, I investigate the effects of rank and kin on female sociability and on the distribution of grooming and association patterns of mothers. I present evidence for a stable female dominance hierarchy determined over a relatively short study period and show that females have distinct social preferences for particular classes of females. I present results supporting the notion that rank effects on reproductive success and sociability are determined by increased access to food resources and energy consumption and provide one benefit for daughters of high-ranking females to remain in their natal community as adults.

In chapter three, I investigate how the diet and sociability of a mother influences the sociability of her offspring. This chapter focuses on the most frequent play partners and social play networks of offspring and how these relate to a mother's association patterns her degree of relatedness to other community members, and her length of residency in the community. The fact that play in chimpanzees is primarily social may be indicative of its function and the examination of most frequent play partners may provide critical information about the adaptive significance of social play (Fagen 1981). This chapter seeks to investigate how social relationships are developed during the lengthy period of immaturity and seeks to explore social and ecological factors influencing the rate of play. Since social relationships among female chimpanzees at Gombe appear distinct in many ways from those of other study sites, investigating these distinctions in terms of their effects on offspring development will broaden our knowledge on the long-term consequences of female status and sociability.

In chapter 4, I investigate further, the nature and possible functions of social play between dependent offspring. Analysis of play video is used to identify key characteristics of social play bouts, while focal data is analysed to study partner choice, age changes and sex differences in play behaviours and behaviours that co-occur with play, primarily coercive ones, which play appears to foster. In this chapter I show that play is not purposeless but appears a competitive, affiliative interaction where play partners appear to compete for mutual and highly desirable goals. I provide evidence to refute claims that play is used by individuals to assess both their and their partner's fighting ability while providing further support for the "social cohesion" and "complex

social skills" function. I show that aggression is an important consequence of play and may be used in this context to gain dominance status.

2 Sociability and Dominance among the Female Chimpanzees at Gombe

2.1 Introduction

2.1.1 The Gombe Females

Traditionally female chimpanzees were considered to form egalitarian relationships with each other and a dominance hierarchy was not thought to be a strategy used to increase female reproductive success because it was assumed intra-group contest competition between females for resources, such as food, did not occur. The fission-fusion nature of chimpanzee society allowed females to adjust to periods of food shortages by allowing them to forage in smaller parties or alone, avoiding one another. Adult female chimpanzees at Gombe however appear to employ behavioural strategies not observed between females at other study sites. Goodall (1986) found that 33% of observed aggression by adult females was directed to other females compared to 0% at Kanyawara in Uganda (Muller 2002) and at Gombe (and also at some other field sites e.g. Nishida 1990 in Pusey, Williams & Goodall 1997, Boesch & Boesch-Achermann 2000) a dominant female or high-ranking females have regularly been identified. Most striking perhaps is the fact that female chimpanzees at Gombe pant-grunt to one another, behaviour rarely observed between parous females at other study sites (e.g. Muller 2002). Pant-grunting is a dominance-related behaviour given by a subordinate to a more dominant individual as affirmation of his/hers relative and subordinate rank position within the dominance hierarchy. Male chimpanzees perform dominance related

behaviours such as pant-grunting to one another relatively often and subsequently the male dominance hierarchy is well defined. While females have been acknowledged to pant-grunt to males, the consensus being that all males are dominant to females, the question of why females should pant-grunt to each other, at Gombe, was not addressed until fairly recently. At best pant-grunting between females was seen as inconsequential because it occurred infrequently compared to pant-grunting between males. However, while the male dominance hierarchy is for the most part well defined, during periods where the dominant position is challenged, rank positions can become less clear-cut and even within periods of stability some rank positions between some individuals are not confidently ascertained. Therefore, while the evidence pointed towards less distinct relationships between females, in terms of the frequency of interactions, it did not rule out the possibility that a female dominance hierarchy existed.

By examining the direction of all pant-grunts between females from 35 years of long-term data, Pusey, Williams & Goodall (1997) not only confirmed the presence of a female dominance hierarchy at Gombe, but most importantly demonstrated that dominance rank influenced various measures of female reproductive success. They also showed that a large proportion of females (50%) remained in their natal community as adults to reproduce instead of dispersing at sexual maturity. As a consequence of female philopatry, the degree of relatedness between females at Gombe should be greater than at other sites where female philopatry is less common. Both female philopatry and the presence of a female dominance hierarchy should affect female social relationships.

Williams, Liu & Pusey (2002), for instance, demonstrated that rank effects on female association patterns resulted in highly differentiated relationships.

2.1.2 Hypothesis to Test

For this chapter the main hypothesis that will be tested is this:

Ha = Sociability among females with offspring is dependent upon rank and kinship.

Ho = A mother's sociability is not dependent upon rank or kinship.

One question of particular interest is, are higher-ranking females more social than lower-ranking females? If high-ranking females feed in nutritionally richer core areas, then they may be able to afford the costs associated with socialising, e.g. costs away from foraging. Lee (1983) argued that conditions of high food availability increased the frequency of social interactions in both vervets and two species of baboons. Another question of interest is whether younger and lower-ranking females have a higher diversity of associates than older, higher-ranking females. This question stemmed from the impression that younger, lower-ranking females appeared to instigate grooming with other adult females more than older, higher-ranking females did. While the two questions appear at first sight to contradict each other, sociability can be defined in a number of ways based on grooming and association patterns with certain classes of individual.

Finally kinship effects on chimpanzee female social relationships is a topic that has received very little attention, primarily because at sites where females disperse at maturity most adult females in any one community are assumed to be unrelated. At Gombe, a high proportion of adult mother-daughter pairs associate closely together, as a

consequence of female philopatry. Therefore, no insight into female social relationships at Gombe can be gained without addressing the topic of kinship. Here I define sociability in terms of the distribution of grooming patterns and association patterns and investigate the effects of rank and kinship on both.

2.1.3 Findings

In this chapter I present evidence for a despotic, stable and consistent dominance hierarchy among the female chimpanzees at Gombe, which can be discerned over a relatively short period. This is important to demonstrate because if status really does confer advantages to females then interactions should occur fairly regularly. I present results that support the notion that the effects of high rank on reproductive success are due to increased access to food and energy intake. Subsequently, I illustrate a benefit for the daughters of high-ranking females to remain in their natal community as adults, as an explanation of why female philopatry is a strategy used at Gombe. Related to this, I show that rank effects on sociability are primarily determined by energy consumption. In contrast to the conventional view that female relationships are undifferentiated, the association patterns and grooming patterns of mothers reveal distinct social preferences for particular classes of females based on rank and kinship. Rather then explaining the low frequency of grooming among adult females as indicative of its lack of importance, I show that females are constrained from grooming other members of the community by the number of dependent offspring they have and the number of dependent offspring is in turn related to the age of the female. This chapter is an overview of female relationships between females at Gombe, using not only data from an 18-month field work period but

an accumulation of knowledge from observing these same family groups for a considerably longer period (1996-2003). The chapter seeks to add to a growing body of literature demonstrating that the traditional view of female chimpanzee behaviour does not sufficiently describe the adult females at Gombe, that strategies employed by females across populations may be more varied than previously assumed and tries to find accurate explanations for why this may be so.

2.2 Methods

2.2.1 Study Population and Field Methods.

Data were collected on the habituated Kasekela chimpanzee community at Gombe National Park in Tanzania. Data have been collected continuously on this community since 1960 and therefore all community members, except for immigrant females, have been followed since birth and infancy. Demographic records have been continually kept and all maternally related individuals are known. I studied this community from 1996 and was therefore familiar with all community members. Data on six parous females were collected between July 2001 and March 2002. The sample was then increased to nine parous females during the second data collection period spanning June 2002 to March 2003. Information on these females and their offspring is shown in appendix one. Data collected on the six parous females, followed during both periods, amounted to 60 hours per female. 30 hours of data were collected on the three parous females included in the sample during only the second fieldwork period. Although the sample size appears small this encompassed 90 % of all mothers with dependent offspring. Data were confined to

parous females with dependent offspring due to the study's main objective of investigating a mother's role in the social experiences of her dependent offspring. Data were collected using focal animal sampling techniques (Altmann 1974). Follows varied in length (from one to eleven hours, with a median of five hours) but mothers and their dependent offspring were normally followed from early morning to nesting time in the evening. Follows were rotated so that all females were sampled at systematic intervals throughout the study period. In practise this proved hard to maintain since mothers varied in their level of habituation; the three shy females who were added to the sample in the second data collection period were hard to find when travelling alone and had to be "opportunistically" followed when they were observed in a group. All but one of these shy females tolerated being followed once they left a party to travel by themselves with their dependent offspring but one of these was only observed during one short three-month period. Thus, due to the challenging nature of following and collecting data on solitary females, systematic data collection was compromised in order to increase the sample size of mothers and collect enough data on each.

General data on party membership, including the identification of cycling females and changes in membership, were collected along with the sexual state of the target female (normally non-cycling and lactating except in two cases), the weather, the approximate location of the target (valley and gully name), and the vegetation type according to Clutton-Brock's (1972 in Goodall 1986) five major types. Data was recorded as these variables changed. In very large mixed groups where changes in party membership were hard to monitor, group membership was recorded at the start and end of the follow.

General behaviour of the female was collected along with the distance of her infant, every minute, on the minute. If she was feeding the food species was recorded along with the type of food. General behaviour provided the context for the following comparatively rare behaviours. These included the identity and distance of her nearest neighbour, the direction and identity of grooming partners, any play and sexual behaviour involving the target and agonistic behavioural patterns involving the target such as pant-grunts, displacements and aggression. Agonistic behaviours between the target female and other females were of particular interest and recorded in detail. All these specific behaviours were recorded regardless of whether they occurred on or off the minute. Behavioural interactions that were indicative of a dominance relationship but did not involve the target females were also recorded *ad libitum* in an effort to assign rank to as many females in the community as possible.

Long-term data were also used, the details of which are described in Williams, Liu & Pusey (2002). Long-term data (entailing ecological, behavioral and locational data) have been collected every day by Tanzanian field assistants in the same format since 1972 and since an individual (male or female) is followed all day until nesting in the evening, the location of at least some community members are known for the following day. Knowledge of the locations of known individuals often influenced the choice of target for that day or the following one. If the locations of no parous females included in this study were known then I actively searched for specific individuals in their known home ranges. Although the solitary nature of female chimpanzees makes it hard to locate them, female ranging patterns can be predicted from the presence of ripe food sources within home

ranges. Knowledge of both individual home ranges and ripe food patches markedly increased the chances of finding specific individuals.

2.2.2 Measures of Dominance

All dyadic dominance interactions that were clear-cut in terms of a winner and a loser were used. I used three separate methods of determining dominance, each of which were based on creating dominance matrices and entering the raw scores of winning interactions.

Following Bramblett (1981) I created a dominance matrix where a +1 was assigned to each cell in which the dyad score indicated a dominant relationship and a –1 indicated a subordinate relationship. If the individuals were not seen to interact or the score did not meet a 75 percent criterion the cell was assigned a zero. The rows were then summed to score status totals for each female where the status score equals the net number of individuals that a subject can dominate (Bramblett 1981). This matrix and the resulting order of rank are shown in figure 1. The second method used was a Lotus-based programme developed by Craig Packer and utilised by Pusey, Williams & Goodall (1997). The raw scores of winning interactions were entered into a matrix and the computer programme generated status scores for all females in the matrix based upon weighted ranks or the number of individuals a specific female dominated. The third method developed by Jameson, Appleby & Freeman (1999) and used by Muller (2002) and Wilson, Hauser & Wrangham (2001) was based upon a mathematical model of

Do	PI	FF	GM	FN	SW	SA	TZ	TA	TT	CD	YD	JF	SS	KP	DL	SIF	BAI	HO	NAS	CF2	MAK	
PI	0	1	1	1	0	0	1	1	1	0	0	0	1	0	0	0	0	0	1	0	0	8
FF	-1	0	1	-1	1	0	0	1	0	1	1	0	0	0	0	1	1	0	1	0	0	6
GM	-1	-1	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0	3
FN	-1	1	-1	0	0	0	-1	1	-1	0	0	0	0	1	1	0	1	0	0	0	0	1
SW	0	-1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2
SA	0	0	0	0	-1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	2
TZ	-1	0	-1	1	-1	-1	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0
TA	-1	-1	0	-1	0	0	-1	0	-1	0	0	0	0	0	1	0	1	0	0	0	0	-3
TT	-1	0	-1	1	0	0	0	1	0	0	-1	0	0	0	0	0	0	0	0	0	0	-1
CD	0	-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-1
YD	0	-1	-1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	2
JF	0	0	0	0	0	0	-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-1
SS	-1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-1
KP	0	0	0	-1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
DL	0	0	0	-1	0	0	0	-1	0	0	0	0	0	0	0	0	0	0	0	0	0	-2
SIF	0	-1	0	0	0	-1	0	0	0	0	0	0	0	-1	0	0	0	0	0	0	0	-3
BAI	0	-1	0	-1	1	-1	-1	-1	0	0	0	0	0	0	0	0	0	0	0	0	0	-4
HO	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
NAS	-1	-1	-1	0	0	0	0	0	0	0	-1	0	0	0	0	0	0	0	0	0	0	-4
CF2	0	0	0	0	0	0	0	0	0	0	-1	0	0	0	0	0	0	0	0	0	0	-1
MAI	0	0	0	0	0	0	0	0	0	0	-1	0	0	0	0	0	0	0	0	0	0	-1

Figure 1: showing Bramblett's (1981) dominance matrix for the female chimpanzees at Gombe. Individual abbreviations are: PI = Patti, FF = Fifi, GM = Gremlin, FN = Fanni, SW = Sparrow, SA = Sandy, TZ = Trezia, TA=Tanga, TT=Tita, CD=Candy, YD=Yolanda, JF=Jiffy, SS=Skosha, KP=Kipara, DL=Dilly, SIF=Sifa, BAH=Bahati, HO=Hope, NAS=Nasa, CF2=California2, MAK=Malika.

paired comparisons and did not assume a strictly linear hierarchy. This method can also predict dominance relationships between individuals who are never observed to interact together. First, initial estimates of scale values s(ai) for each individual were calculated from the following equation

$$s(ai) = [c(2Wi-Ni)/2Ni]$$

where c is a constant equal to 2.50663; Wi is the number of encounters in which animal ai was observed to have won; and Ni is the number of encounters in which ai was involved (Jameson, Appleby & Freeman 1999). Then a second mathematical equation was applied repeatedly to observed data until scores converged and continuing calculations no longer induced changes.

$$s(ai) = [2(Wi-Li)/Ni]+Qi$$

where Li is the number of encounters in which animal ai lost; and Qi is the mean scale score of those animals that ai met in agonistic encounters (Jameson, Appleby & Freeman 1999). A portion of the derived calculations, are shown in figure 2.

	PI	FF	GM	FN	SW	SA	TZ	TA	TT	CD	YD	KP	DL	SIF	BAH	NAS	MAK	JF	CF2	WI	LI	Ni	s(al)0	QI 0
PI	x	5	4	2			1	5	2	2						1				22	0	22	1.25	-0.282
FF		x	5		2	1	1	2		1	2				2	1				17	7	24	0.52	0.074
GM			x	2			1	3	5		1					1				13	12	35	-0.32	0.017
FN		2		x				4					1	1	2	2				12	7	19	0.33	-0.38
SW					x		2	4							1					7	2	8	0.94	0.086
SA						x		7							3		1			11	4	15	0.58	-0.168
TZ				1			x	6							5			1		13	14	27	-0.05	-0.066
TA			3	1				x					2		1					7	22	29	-0.65	0.064
TT				1				2	x											3	8	11	-0.57	0.01
CD										x										0	3	3	-1.25	1.01
YD									1		x					1	1		1	4	3	7	0.18	-0.396
KP												x		1						1	1	2	0	-0.462
DL													x							0	3	3	-1.25	-0.322
SIF														x						0	1	1	-1.25	0
BAH															x					0	14	14	-1.25	0.251
NAS																x				0	6	6	-1.25	0.382
MAK						1														1	2	3	-0.42	0.45
JF																				0	1	1	-1.25	-0.046
CF2																				0	1	1	-1.25	0.179

Figure 2: showing the dominance matrix and some of the calculations involved in determining status scores using a method developed by Jameson, Appleby & Freeman (1999). Individual abbreviations are: PI = Patti, FF=Fifi, GM=Gremlin, FN=Fanni, SW= Sparrow, SA=Sandy, TZ= Trezia, TA=Tanga, TT=Tita, CD=Candy, YD=Yolanda, JF=Jiffy, SS=Skosha, KP=Kipara, DL=Dilly, SIF=Sifa, BAH=Bahati, HO=Hope, NAS=Nasa, CF2=California2, MAK=Malika.

2.2.3 Measures of Association

I used four measures of association patterns:

The non-focal association measure measured the proportion of time when the target and her dependent offspring were not the focal, spent in a party of any composition. This measure was calculated from focal follow data. Definitions of party types followed Goodall (1986). This measure is somewhat analogous to Williams, Liu & Pusey's (2002) focal association measure. Focal data was not used since three of the mothers were not well habituated, could often only be located when they joined a party and could not always be followed once they left a party. Using focal data would have overestimated the total time that these three females in particular spent in groups. The resulting measure was then expressed as a percentage. The non-focal association measure, I regard as a general measure of an individual's likelihood of joining a party and therefore her sociability. One assumption that this measure makes, however, is that females not observed in a party were associating alone with their dependent offspring. Since

sociability among females is affected by sexual state, I controlled for the fact that one female was cycling during a part of the study by omitting follows where she had a sexual swelling. Another parous female had an abnormal cycling pattern, swelling on a regular basis even before she had weaned her infant. All follows were included, although the swelling probably altered her sociability with other group members. Certainly human researchers could only follow her alone when she had a sexual swelling.

Each female's level of sociability with adult males was measured in terms of the *male association measure* also used by Williams, Liu & Pusey (2002). I recorded the amount of time females were encountered during focal male follows (i.e. were present in mixed groups) as a proportion of the total time that males were followed. I used male follows from Gombe's long-term data that occurred within the two time periods of this study.

To measure levels of association between females, I used the *dyadic association measure.* This is a modified version of the one used by Boesch & Boesch-Achermann (2000), based on the simple ratio association index described by Cairns & Schwager (1987). This is described well by Williams, Liu & Pusey (2002) and is calculated as follows:

% Association =

$$\frac{\text{\# times A first arrived with B's first arrival (AB)}}{\text{(total first arrival of A (AT)) + (total first arrival of B (BT)) – (first arrivals of A with B(AW)) – (first arrival of B with A (BW)) + (\# times A first arrived with B's first arrival (AB)) – (\# times they arrived in the same follow but not together, A first (AP)) – (\# times they arrived in same follow but not together, B first (BP))}} \times 100$$

Instead of considering the amount of time dyads spent together, this calculation takes into account just the first sighting of a pair. The first time in a day when the focal met an individual was extracted and then for each dyad the proportion of all their arrivals within 5 minutes of each other was determined. This assumed that all animals that arrived within 5 minutes of each other were together when encountered by the focal animal (Williams, Liu & Pusey 2002).

Grooming patterns were investigated by calculating the proportion of grooming time that target females gave to or received from another individual, relative or non-relative, of particular age, rank and sex. Grooming patterns can be especially illuminating in terms of identifying individuals or classes of individuals that females are attracted to. Although grooming patterns among male chimpanzees have been investigated, grooming patterns among females have received little attention since the low rate with which social

grooming is performed has led to an assumption that it is a relatively unimportant component of female behaviour.

Since female sociability may be affected by diet quality, I expanded my analysis to look at the relationship between diet, rank and sociability. I defined diet quality as the proportion of fruit and palm nuts consumed and expressed this as a percentage. This measure was calculated from data collected during focal follows. Since three of the nine mothers were only followed during the second fieldwork period, I limited analysis of diet data to this period and excluded one of these three from the analysis since she was followed only during a short three-month period characterised by food scarcity. Seeking an appropriate measure of diet quality is difficult since the actual nutrient and energy content in different chimpanzee foods has not yet been quantified and measured. However, although few analyses of fruit nutrient content are available, fruit are generally rich in readily metabolizable sugars (Isabirye-Basuta 1988). The duration of fruit feeding bouts gives only a rough estimate of actual energy intake but along with durations of feeding per se should indicate increased nutrient acquisition or decreased feeding efficiency (Isabirye-Basuta 1988). As an alternative definition of diet quality I investigated the proportion of vegetable matter (leaves, vines, and flowers) consumed. I assumed that vegetable matter contributes very little to the energy requirements of an individual and therefore a larger proportion of vegetable matter in the diet, measured in terms of the duration of feeding bouts, was an indication of a sub-optimal diet. This assumes chimpanzees substitute vegetable matter for higher energy foods, if they can't

consume the latter but there is reason to suspect that female chimpanzees consume vegetation for other non-nutritional reasons (Wallis 2002).

2.2.4 Analysis

Statistical analysis was performed with the SPSS statistical package. Due to low sample size analyses utilised non-parametric tests. For seven females missing data constituted between 1-10% of focal data, whereas for two, it constituted less than 14%. Overall missing data was assumed to be within acceptable limits and therefore the data was not corrected. Correlations were tested with Spearman's rho. The Mann-Whitney U test and the Wilcoxon signed ranks tests were utilised in analyses involving two independent and dependent groups, respectively. All statistical tests were two tailed, with an exact significance threshold of 0.05. Tendencies were defined as tests that yielded a significance threshold of less than 0.1.

2.3 Results

2.3.1 Dominance

I recorded a total number of 141 independent aggressive incidents and dominance interactions between or involving females in 18 months of fieldwork. Most but not all of these were dyadic. Almost half of these, 46% occurred in a feeding context (a value similar to that reported by Goodall of 38%), 29% occurred in a greeting context, where two individuals met up while travelling, 13% involved offspring support and 2% occurred when females formed coalitions against males. 10% I identified as power

conflicts defined as any high-key interaction (overt aggression, attack, display, chase), which appeared as an unprovoked show of dominance.

62% of interactions within the feeding context involved low-key behaviours: pant-grunt, avoidance, displacement or a present, or a combination of these. The majority of low-key interactions, 30% of interactions in the feeding context, involved the subordinate individual pant grunting to the more dominant one. Only 8% involved one individual actively avoiding another, suggesting that avoidance, at least while in close proximity, isn't a strategy used very often among female chimpanzees at Gombe. 79% of all interactions within a greeting context involved a subordinate female pant grunting to a higher-ranking female. As with males then, pant grunting between females appears to be used as a formal sign of submission (de Waal 1982) and as a way of re-establishing a relationship after absence. 87% of interactions involving offspring support were high-level responses involving chases, displays and fights, as might be expected if the motivation is the defence of young. 41% of these involved Trezia's support of her juvenile son Zeus who was often aggressive towards other females. Trezia supported her son in disputes far more than any other female with a juvenile son and it was questionable whether the interaction was purely in defence and support, or as an immigrant with no kin in the community, a strategy to exert her dominance or gain future support from her son. 95% of all interactions defined within a power context involved high-level behaviours.

In 25% (n = 26) of interactions involving high-key behaviours, not including interactions involving the support of offspring, the aggressor had close adult kin in close proximity. In

39% of the interactions (n = 9), adult male or female kin actively supported the aggressor, five by female kin, three by male kin, and one by both male and female kin. In 14%, nonkin supported aggressors. In 11% (n = 3) of the interactions close kin were not in close proximity to the aggressor and the aggressor did not receive support. In only 7% of the interactions (n =2) the aggressor did not have kin in the community and did not receive support. This highlights the importance of adult kin in terms of providing support during high-level conflicts.

107 dyadic interactions were used to determine rank. All interactions involved both high and low key behaviours as described above. Results differed depending on which method was used to generate status scores. Only two females, Patti and Fifi, were consistent in their position as alpha and second highest-ranking female, respectively. Depending on the magnitude of the status scores generated under each method, I classed each of the nine females sampled into one of six ordinal ranks: high-high, high, high-middle, middle, high-low, low. This resulted in three ordinal ranks for each female. Since at least two of the three ranks were the same I was able to take the mode value and order the females into a hierarchy of relative rank. Three females had the same ordinal mode value (middle), so I compared the three ordinal ranks for each female against the other two females in order to determine their relative rank. The resulting rank matched nicely to my own impressions of female relationships and is shown in Table 1. The following analysis was done with this order of relative rank.

Female	ID	Bramblett's score & ordinal rank		Packer's score & ordinal rank		Freeman score & ordinal rank		Mode	Rank
PATTI	PI	8	HH	24	HH	1.9	H	HH	1
FIF	FF	6	H	17.2	H	1.1	H	H	2
SANDY	SA	2	M	4	L	0.8	HM	M	4
GREMLIN	GM	3	HM	12.5	M	0.2	HM	HM	3
FANNI	FN	1	M	9.44	M	0	M	M	5
YOLANDA	YD	2	M	2	L	0	M	M	7
TREZIA	TZ	0	M	5.6	HL	0	M	M	6
TANGA	TA	0	L	3.4	L	-1	HL	L	9
TITA	TT	-1	HL	5.6	HL	-1	HL	HL	8

Table 1: showing the resulting status scores generated from three different methods. From the three sets of status scores, ordinal ranks were calculated and from the three sets of ordinal ranks, a mode value taken in order to establish the order of relative rank. HH =high-high; H = high; HM = high-middle; M = middle; HL = high-low; L = low. In terms of relative rank 1 = highest and 9 = lowest.

The rank of a mother was significantly correlated to her age (Spearman rho = 0.95; n = 9; $p < 0.01$). Older parous females obtain higher rank (figure 3). This is in agreement with Pusey, Williams & Goodall (1997), who found that individual dominance rank increases with age for all females and Nishida (1990 in Pusey, Williams & Goodall 1997), who found the same patterning of relationships in the female chimpanzees at Mahale Mountains, about 200 kilometres south of Gombe.

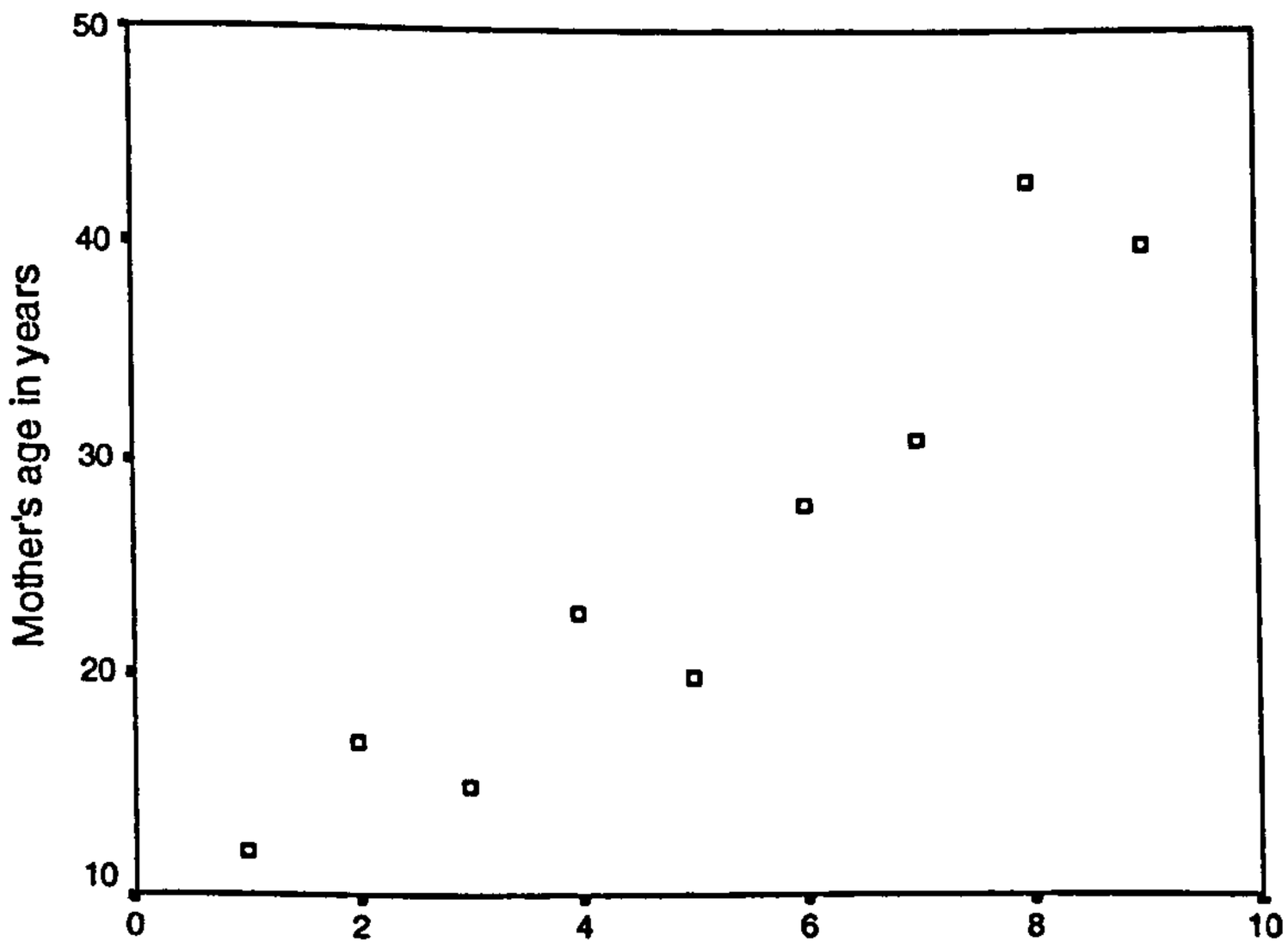


Figure 3: Scatter-plot showing a linear relationship between a parous female's age and her relative rank position. 1 = lowest, 9 = highest rank position.

Summary

1. 141 independent aggressive and dominance interactions between females were recorded in 18 months of fieldwork: far more than that recorded at another East African site, Budongo Forest, Uganda.

2. Almost half of all these interactions (46%) occurred in a feeding context.

3. The majority of interactions in the feeding and greeting context involved pant grunting between females, suggesting that pant grunting is used more often between females at Gombe than between females at some other sites.

4. The presence or potential support of adult kin may determine the kind of response given by a female to another female. Most high-level responses (chase, fight attack etc.) occurred when kin were either in close proximity or gave their active support.

5. Ranking of mothers into a linear hierarchy was achieved and rank was highly correlated to age. Older mothers gained higher rank.

Having identified a dominance hierarchy the following section seeks to explore the benefits of high rank. If females are really competing among themselves for superior food resources then higher-ranking females should consume higher quality diets than lower-ranking females. Such differences could have consequences for a mother's ability to socialise, if there are real costs of grouping, such as decreased foraging efficiency caused by increased scramble competition or more time spent in other activities.

2.3.2 General Sociability and Diet

Since data collection on all target females did not occur as systematically as hoped, sources of inter-individual differences (such as rank, age, etc.) on diet quality may be biased by random sampling errors, if some females were over- or under-sampled during peak versus non-peak feeding times. To investigate this I first sought evidence for peak feeding times during the day. If peak times existed then inter-individual differences in

diet quality could be corrected by weighting for the percentage of time observed during peak versus non-peak periods. Feeding rates across the day are shown in figure 4.

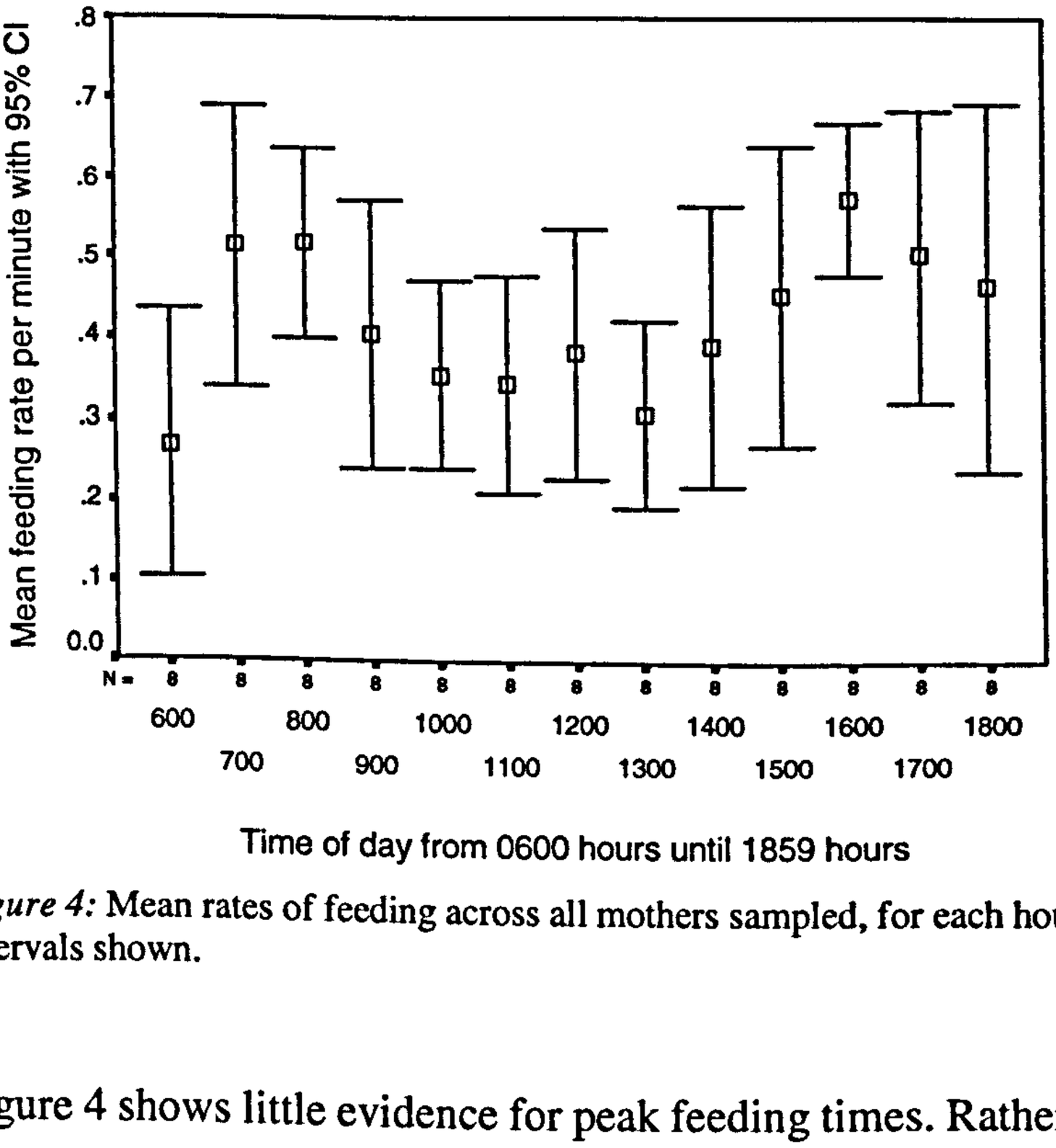


Figure 4: Mean rates of feeding across all mothers sampled, for each hour of the day, with 95% confidence intervals shown.

Figure 4 shows little evidence for peak feeding times. Rather females appear to feed continually throughout the day. The means shown are tightly distributed and all confidence intervals overlap, suggesting that no feeding peaks occur consistently over all individuals. Therefore differences in the distribution of observations are highly unlikely to bias feeding rates, since feeding occurs constantly throughout the day.

High-ranking females and their adult daughters who had not emigrated out of the natal community spent a significantly greater proportion of their time in a group than the other mothers in the sample (Mann-Whitney U = 1.00; n1= 4 mothers; n2 = 5 mothers; $p < 0.05$ 2-tailed) as shown in figure 5. These females consisted of the alpha female, Patti and the beta female, Fifi and their respective adult daughters, Tanga and Fanni. Fanni was ranked

as the fifth highest ranking female in the hierarchy of relative rank, constructed above for all mothers in the study sample, while Tanga was ranked ninth, in last place.

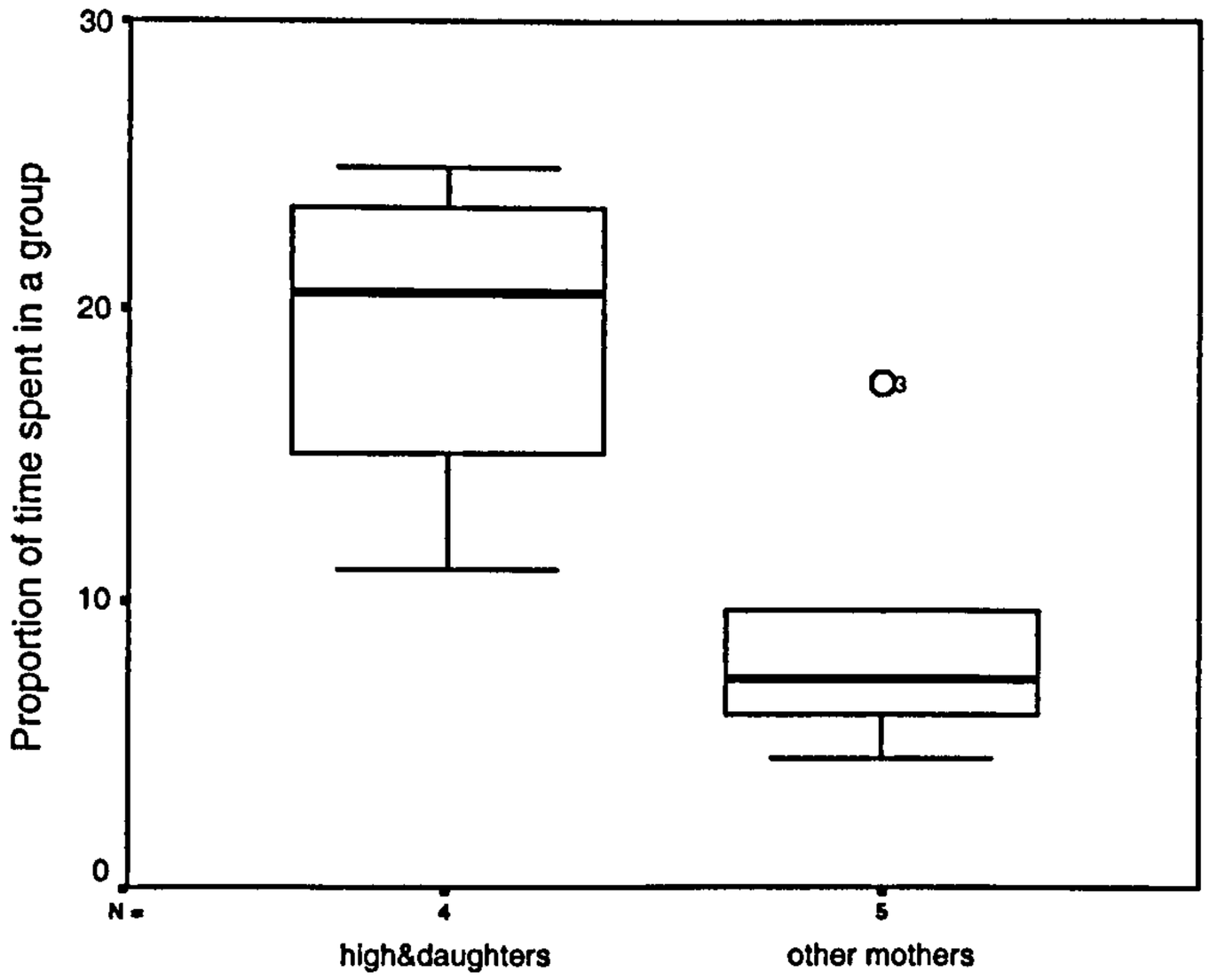


Figure 5: Box plot showing the proportion of time observed in a group, between two groups of mothers: high-ranking mothers and their adult daughters who had never dispersed, and all other mothers. Each plot shows the median, quartiles and outliers within a category.

It was possible however that high- ranking mothers and their adult daughters only appeared more social because they were spending a large proportion of this time associating with each other. To investigate this, and following Williams, Liu & Pusey (2002), I redefined Goodall's (1986) definitions more strictly as the proportion of the total study period that individuals spent in parties of non-maternally related individuals. There was a strong tendency for high-ranking females and their adult daughters to spend a greater proportion of time in parties than other parous females (Mann-Whitney U = 3.00; n1 = 4; n2 = 5; $p<0.1$, 2-tailed).

There was no significant relationship between relative rank and diet quality defined in terms of the proportion of fruit and palm nuts consumed (Spearman's rho = -0.214; n = 8; p>0.05, 2-tailed). However, high-ranking females and their adult daughters consumed significantly higher proportions of fruit and nuts in their diet than the other mothers sampled (Mann-Whitney U = 0.00; n1 = 4; n2 = 4; p< 0.05, 2-tailed) and therefore spent a greater proportion of their focal feeding time feeding on high-energy foods (see figure 6). They did not however spend a significantly greater proportion of their total time feeding (Mann-Whitney U = 6.00; n1 = 4; n2 = 4; p > 0.05, 2-tailed), which suggests that they were more efficient feeders in terms of consuming an energy rich food supply, than other females. The proportion of fruit and palm nuts consumed was correlated to the proportion of vegetable matter consumed (Spearman's rho = - 0.69; n = 8 mothers; p = 0.058, 2-tailed).

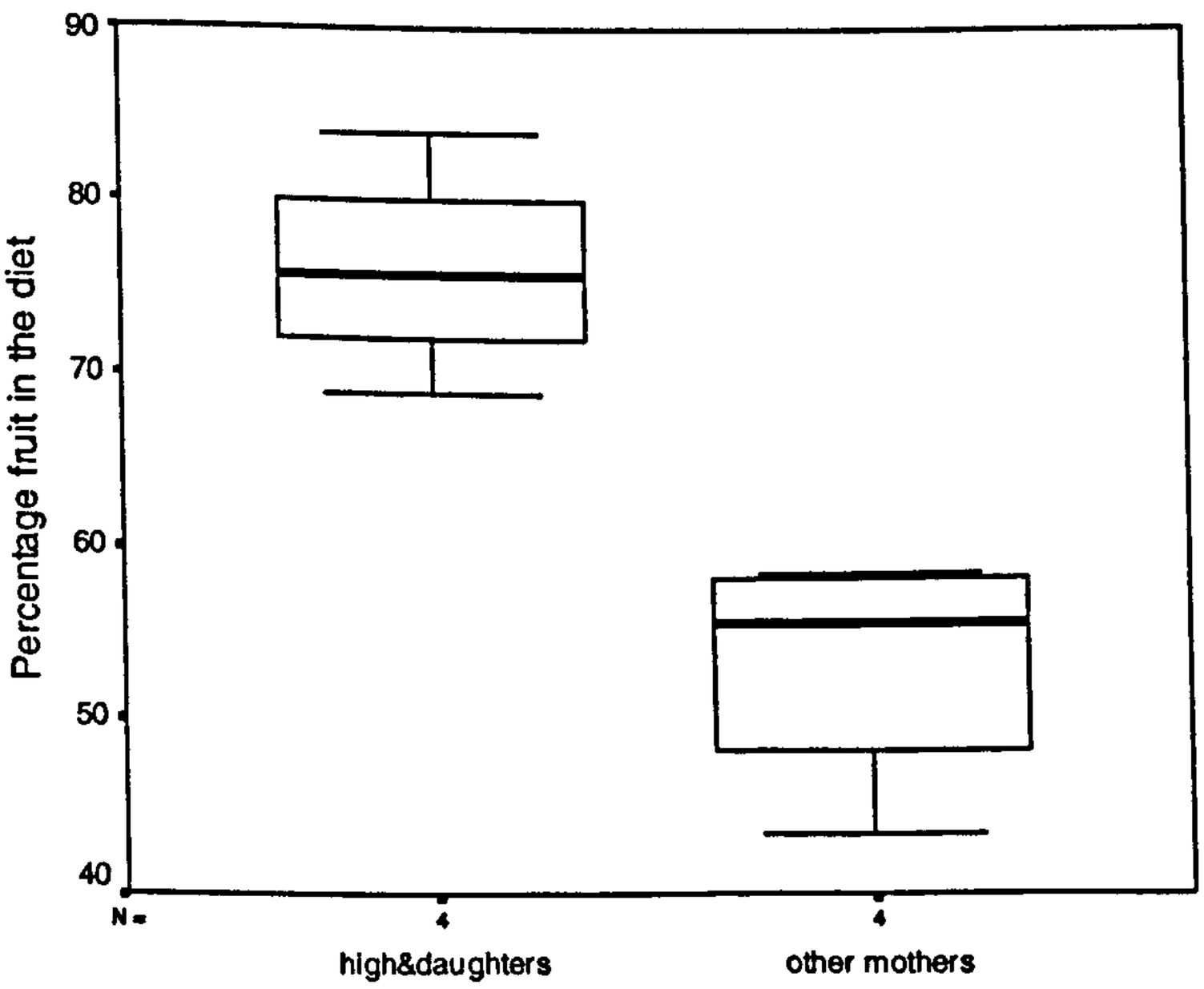


Figure 6: Box plot showing the proportion of fruit and palm nuts in the diets of high ranking females and their adult daughters who did not emigrate and all other mothers. Each plot shows the median and quartiles within a category.

Females who ate more fruit showed an extremely strong tendency to eat less vegetable matter and high ranking females and their adult daughters also showed a tendency to consume less vegetable matter than other females (Mann-Whitney U = 2.00; n1 = 4; n2 =

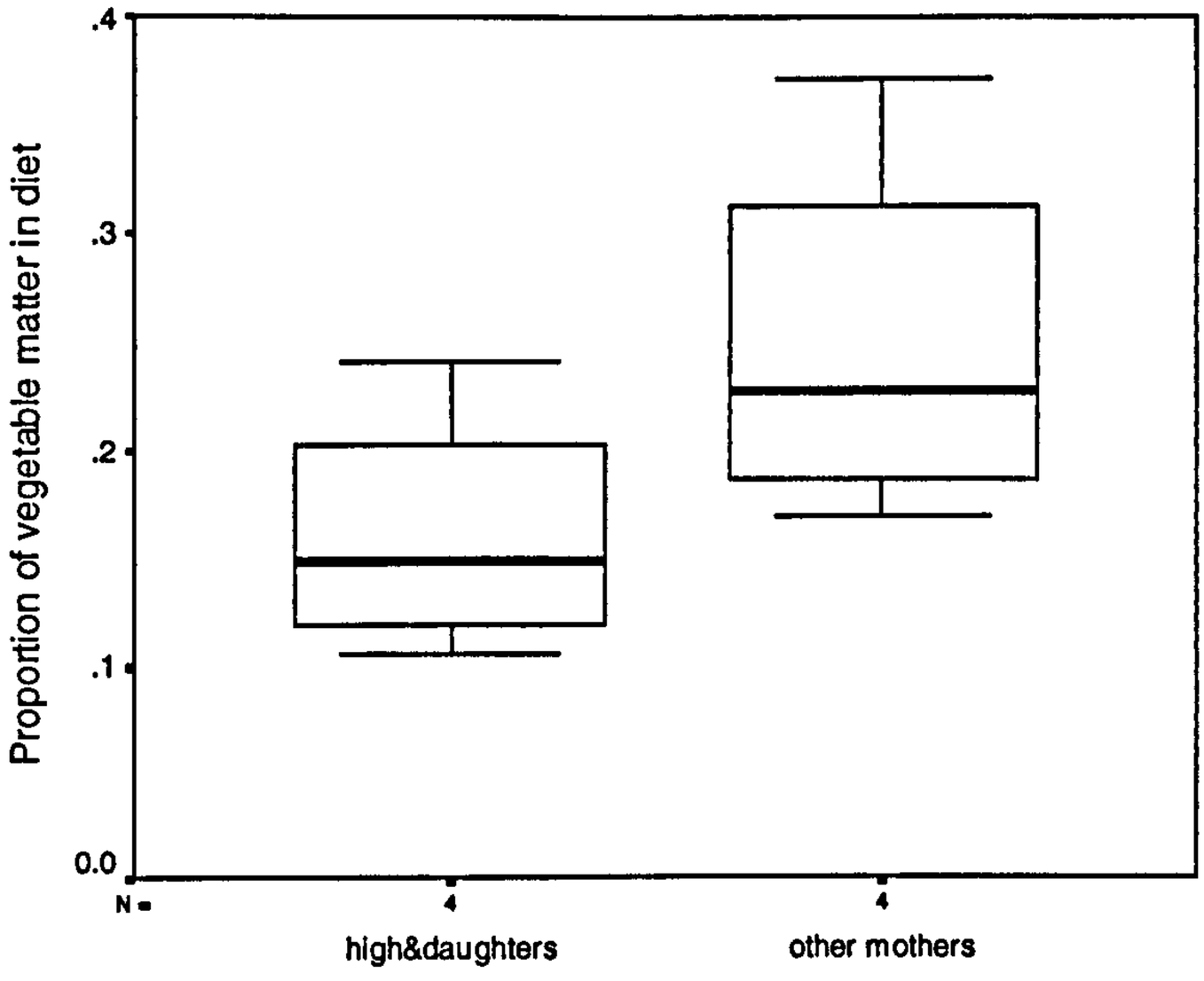


Figure 7: Box plot showing the proportion of vegetable matter (leaves, flowers, shoots and vines etc.) eaten by high-ranking females and their adult daughters who had not emigrated (n = 4) and other mothers in the community. Each plot shows the median and quartiles within a category.

4; p = 0.1, 2-tailed). Mothers who ate more fruit and palm nuts in their diet were significantly more social (Spearman's rho = 0.738; n = 8; p< 0.05, 2-tailed), although when sociability, computed for just the second fieldwork period, was compared, only a tendency remained (Spearman's rho = 0.667; n = 8; p< 0.1, 2-tailed). Mothers who ate more vegetable matter also showed a tendency to be less social (Wilcoxon T+ = 36; n = 8 mothers; p < 0.01, 2-tailed). These results suggest that either, high-ranking females and their adult daughters are more social because due to a high-energy diet they can afford the costs of grouping, or larger groups can monopolize larger food sources. To investigate this I determined the proportion of time in parties which mothers spent

feeding on fruit and compared this to the proportion of alone time feeding on fruit (figure 8). If mothers spent a greater proportion of their alone time feeding on fruit this would suggest that mothers with higher quality diets could afford the costs of socialising in groups, such as costs related to time away from foraging. Mothers spent a significantly greater proportion of their alone time feeding on fruit than their time in a group (Wilcoxon signed ranks $T+ = 3$; $n = 9$; $p < 0.05$, 2-tailed) supporting this hypothesis and suggesting that females maximise their feeding efficiency by feeding alone (Wrangham 1979b in Pusey 1983).

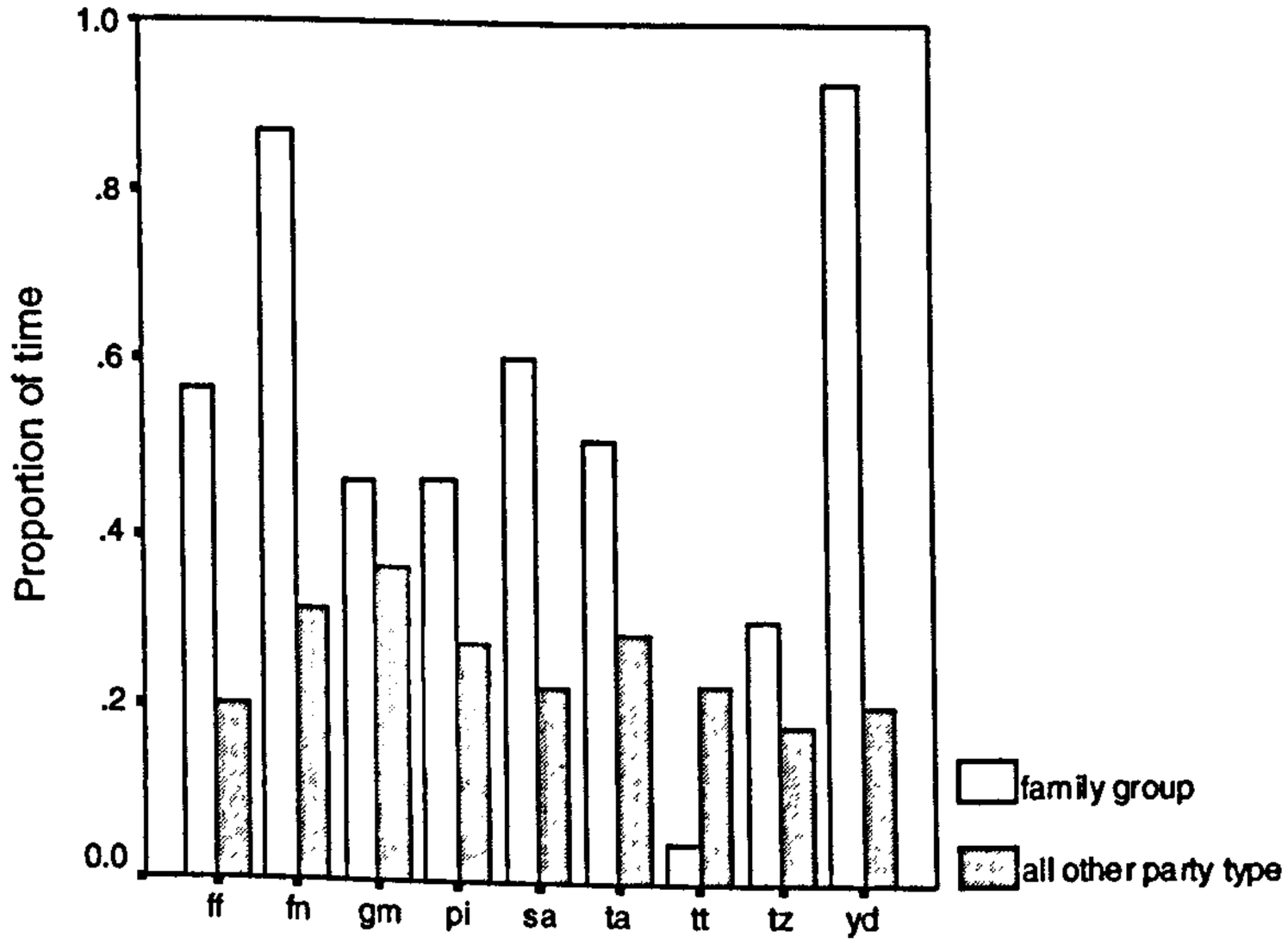


Figure 8: Proportion of alone time (with dependent offspring) spent feeding on fruit compared to the proportion of time in a party spent feeding on fruit, for nine parous females. ff= Fifi, fn = Fanni, gm = Gremlin, pi = Patti, sa = Sandy, ta = Tanga, tt = Tita, tz = Trezia, yd = Yolanda.

Summary

1. There was an interaction of rank and kin affects on sociability. High-ranking females and their adult daughters who remained in the natal community as adults spent more time in groups.

2. There was an interaction of rank and kin affect on diet quality. High –ranking females and their adult daughters who remained in the natal community as adults consumed a

greater proportion of high-energy foods (fruit and palm nuts) but did not spend more time feeding suggesting they were more efficient feeders in terms of energy consumed.

3. The proportion of time spent in groups appeared determined by diet quality. Mothers who ate a greater proportion of fruit and palm nuts were able to afford the costs of socialising (such as costs away from foraging).

4. Females maximise their feeding efficiency by foraging alone and some aspects of sociability are determined by feeding efficiency.

The proportion of time spent in a group is only one measure of sociability. The following two sections investigate association patterns. The first, female-female association patterns, seeks to show that females have specific preferences among themselves, providing further evidence against the traditional viewpoint that female-female relationships are undifferentiated and supporting the view that contest competition may be an important component of feeding competition among females. Complementary to this, the second investigates female-male association patterns as a comparison and tries to identify some of the factors that determine female-male association.

2.3.3 Sociability between Females

Mother	Rank	Age	Mean w mothers	Std dev w mothers	Mean w other females	Std dev w other females	Overall mean	Overall std dev
PI	1	40	0.13	0.08	0.08	0.05	0.1	0.07
FF	2	43	0.21	0.05	0.16	0.11	0.18	0.09
GM	3	31	0.17	0.07	0.1	0.06	0.14	0.07
SA	4	28	0.18	0.12	0.09	0.06	0.14	0.1
FN	5	20	0.24	0.11	0.15	0.1	0.19	0.11
TZ	6	23	0.14	0.04	0.11	0.06	0.12	0.06
YD	7	15	0.13	0.04	0.09	0.05	0.11	0.05
TT	8	17	0.18	0.04	0.13	0.1	0.15	0.08
TA	9	12	0.2	0.06	0.12	0.08	0.16	0.08

Table 2: shows mother's name, her rank and age, her mean association index and standard deviation, with other mothers and her mean association and standard deviation with other females without dependent offspring. FF= Fifi, FN = Fanni, GM = Gremlin, PI = Patti, SA = Sandy, TA = Tanga, TT = Tita, TZ = Trezia, YD = Yolanda. Rank 1 = highest relative rank; rank 9 = lowest relative rank.

Age was not correlated with the mean DAI (dyadic association index) for nine mothers (Spearman rho = - 0.109; n = 9; p > 0.05, 2-tailed) and neither was rank (Spearman rho = 0.192; n = 9; p > 0.05 2-tailed). Mother and adult daughter pairs associated most together. The mean association for this group was 0.27 (sd = 0.14; n = 5) whereas for maternally unrelated females the mean was 0.13 (sd = 0.076; n = 135). The mean association of dyads composed of parous females with dependent offspring was 0.175 (sd = 0.75; n = 45), whereas for dyads composed of a mother and a female without dependent offspring the mean was 0.12 (sd = 0.788; n = 90). All mothers associated significantly more with other mothers than other females without dependent offspring (Wilcoxon signed ranks T+ = 0; n = 9; p = < 0.01, 2-tailed), supporting findings by Williams, Liu & Pusey (2002), who found that established females, mothers who showed high site fidelity and who had lived in the community for many years, associated significantly more together than with immigrants. Even when relatives were excluded from the analysis the effect was still very significant (Wilcoxon signed ranks T+ = 0; n = 9; p < 0.01, 2-tailed).

There was a high correlation between the DAI of a mother with another mother and the same mother with a female without dependent offspring (Spearman rho = 0.835; n = 9; p< 0.01, 2-tailed). Therefore mothers who showed high associations with other mothers also showed high associations with females in general (see figure 9). There was a correlation between the mean DAI and the percentage of time mothers spent in parties of any composition, which almost reached significance (Spearman rho = 0.653; n = 9; p = 0.057, 2-tailed). Females who spent more time in parties also tended to be more social towards other females. The mean DAI for each mother was not however correlated with

diet quality, defined as the proportion of fruit and palm nuts in the diet, (Spearman rho = 0.539; n = 8; p = 0.168, 2-tailed).

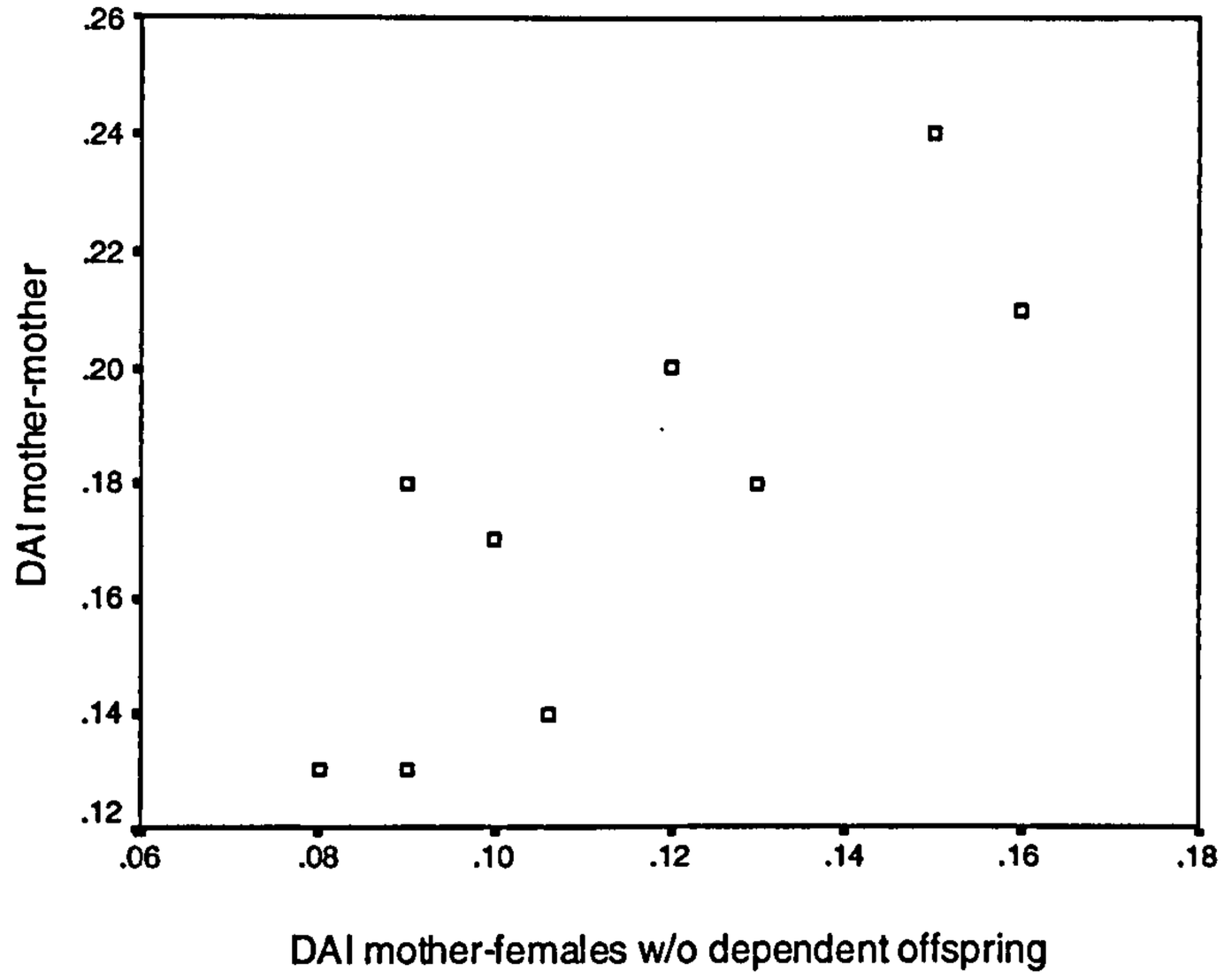


Figure9: Scatter plot showing a linear relationship between the mean DAI of a mother with a mother and the mean DAI with a female without dependent offspring.

Summary

1. Mother and adult daughter pairs associated the most together.

2. All mothers associated significantly more with other mothers than with females without dependent offspring.

3. Mothers who associated more with other mothers also associated significantly more with females in general.

4. Mothers who associated more with females in general also spent a greater proportion of their time in parties.

5. Association between females was not determined by age, rank or diet quality, defined as the proportion of high-energy foods consumed.

2.3.4 Sociability with Males

Rank was not correlated to the proportion of time parous females with dependent offspring spent with males (Spearman's rho = 0.267; n = 9 mothers; p> 0.05, 2-tailed). There was no significant difference between the sociability of mothers with males and that of females without dependent offspring (Mann-Whitney U = 47.00; n1 = 10; n2 = 10; p >0.05, 2-tailed). Even when I categorised females as mothers with dependent offspring, parous females without dependent offspring and nulliparous females, there was no significant difference between the three groups (Kruskall-Wallis chi-square = 0.09; n1 = 10 mothers; n2 = 4 nulliparous; n3 = 6 parous; p >0.05, 2-tailed). This was especially surprising since sex differences in gregariousness, due to parity, have been found (see Wrangham 2000).

I also investigated the impact of offspring on a mother's sociability with males since there is evidence that females who socialise more with males produce male offspring who acquire higher rank as adults (Williams, Liu & Pusey 2002) and juvenile males, by leading their mothers into groups could significantly influence the association patterns of their mothers (Pusey 1983). I compared the sociability of mothers whose oldest juvenile/early adolescent offspring was male to all other mothers. Although there was a slight tendency for this group to spend more time with males this effect was not significant (Mann-Whitney U = 7.00; n1 = 4; n2 = 5; p > 0.05, 2-tailed). There was a greater tendency for mothers whose eldest offspring was a male, including male infants, to socialise more with adult males but again this was not significant (Mann-Whitney U = 3.00; n1 = 6; n2 = 3; p > 0.05, 2-tailed). The average association of mothers with all other

females were highly correlated to their association with males (Spearman rho = 0.929; n = 9; $p < 0.001$, 2-tailed). Mothers who were more social with other females were also more social with males (figure 10). Unlike sociability between females however, there was no significant correlation between a female's sociability with males and the proportion of time she spent in a group (Spearman rho = 0.45; n = 9; $p > 0.05$, 2-tailed). There was also no correlation between a mother's sociability with males and the proportion of her grooming time allocated to each male on average (Spearman's rho = -0.217; n = 9; $p>0.05$, 2-tailed), suggesting that females who socialise most with males don't groom them more on average.

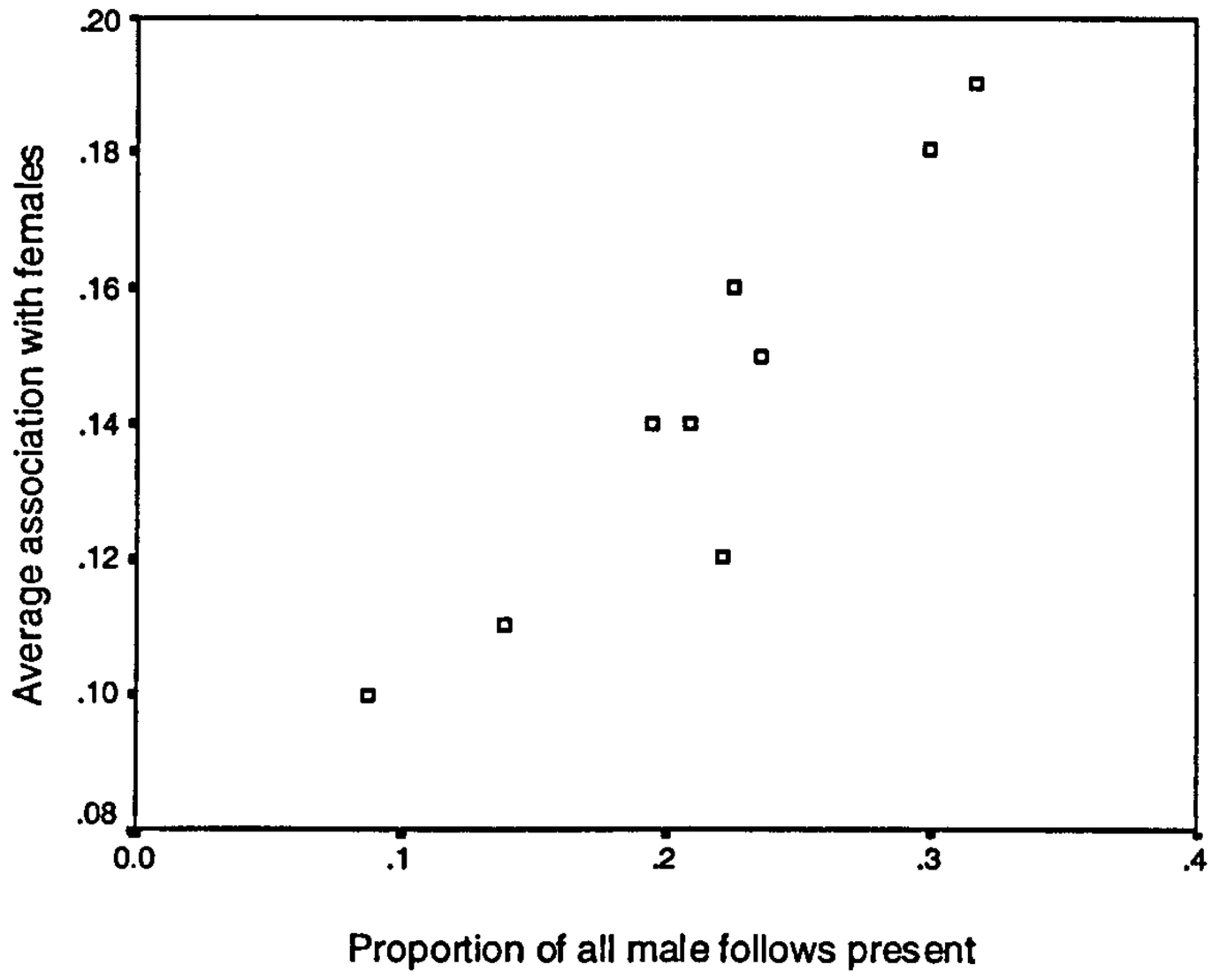


Figure 10: Scatter graph showing a linear relationship between association with both males and females for nine mothers. Association with adult males was measured in terms of the *male association measure* (Williams, Liu & Pusey 2002). Average association with females was taken as the mean DAI with all other females.

Summary

1. Female association with males was not determined by female parity.

2. Female association with males was not determined by the sex of her dependent offspring although there was a slight trend for mothers whose eldest dependent offspring was a male to associate more with the adult males.

3. Mothers who associated more with females also associated more with males.

4. There was no relationship between association with males and the proportion of time spent in a group for all mothers sampled.

5. Females who associate more with males do not groom them more on average.

Traditionally grooming among female chimpanzees has received little attention because it occurs at a much lower frequency than that between adult males and has therefore been considered an unimportant aspect of female sociability. The next section takes a closer look at grooming preferences among mothers, seeks to identify directionality in grooming behaviour and attempts an alternative explanation to why grooming among adult females is comparatively rare. If females truly have specific social preferences then these should be expressed within their grooming patterns.

2.3.5 Grooming

Mothers spent on average 10.44% of their total time grooming socially, although the range was large (5.71% - 20.15%) suggesting that mothers vary greatly in the amount of time that they groom (table 3). There was no correlation between rank and time spent grooming (Spearman rho = 0.383; $p>0.05$, 2-tailed). Table 4 shows the percentage of grooming time allocated to different classes of individuals, giving a clearer indication of grooming distribution between classes of grooming partners.

mother	age	rank	% TIME GROOM	A males	A male relatives	A male nonrelat.	A females	A female relatives	A female nonrelat.	Dependent offspring
PI	40	1	5.71	0.59	0	0.59	1.74	**1.42**	0.318	3.7
FF	43	2	9.83	4.17	**3.49**	0.68	0.00897	0.008	0.00097	6.72
GM	31	3	11.19	1.02	0.975	0.048	0.43	0	0.43	10.38
SA	28	4	6.71	1.04	0.12	0.92	0.17	0.17	0	6.06
FN	20	5	7.11	1.04	0.25	0.79	1.67	1.1	0.57	4.47
TZ	23	6	**20.75**	0.93	0	0.93	0.98	0	0.98	**19.17**
YD	15	7	9.62	3.62	0	3.62	0.52	0	0.52	6
TT	17	8	13.24	**10.21**	0	**10.21**	1.62	0	1.62	1.27
TA	12	9	9.8	1.1	0	1.1	**4.3**	1.3	**3**	3.6

Table3: shows the percentage of total time observed grooming (% time GROOM) in groups of any composition, omitting family groups of mothers and just their dependent offspring (for nine mothers) and the percentages allocated to different groups. A males = adult males; A male relatives = adult male relatives; A male nonrelat. = adult male nonrelatives; A females = adult females; A female relatives = adult female relatives; A female nonrelat. = adult female nonrelatives; dependent offspring = dependent offspring. Not all percentages add up across rows since often more than two individuals were observed grooming simultaneously. FF= Fifi, FN = Fanni, GM = Gremlin, PI = Patti, SA = Sandy, TA = Tanga, TT = Tita, TZ = Trezia, YD = Yolanda. Rank 1 = highest rank, rank 9 = lowest.

mother	age	rank	A males	A male relatives	A male nonrela.	A females	A female relatives	A female non rela.	depend. offpsring	relatives: adults & offpsring
PI	40	1	10.3	0	10.3	30.47	**24.89**	5.58	64.8	89.69
FF	43	2	**42.47**	**35.56**	6.91	9.14	8.15	0.99	68.4	**112.11**
GM	31	3	9.15	8.72	0.43	3.83	0	3.83	**92.77**	**101.49**
SA	28	4	15.47	1.8	13.67	2.52	2.52	0	90.29	94.61
FN	20	5	14.58	3.57	10.12	23.52	15.48	8.04	62.8	81.85
TZ	23	6	4.46	4.46	0	4.72	0	4.72	**92.38**	92.38
YD	15	7	37.63	0	37.63	5.38	0	5.38	62.37	62.37
TT	17	8	77.13	0	**77.13**	12.23	0	12.23	9.57	9.57
TA	12	9	11.06	0	11.06	**43.3**	13.18	**30.12**	36.47	49.65

Table 4: Showing the percentage of grooming time allocated to different classes of individual. PI = Patti; FF = Fifi; GM = Gremlin; SA = Sandy; FN = Fanni; TZ = Trezia; YD = Yolanda; TT = Tita; TA = Tanga. Rank 1 = highest rank, rank 9 =lowest.

There was a tendency for mothers to groom their dependent offspring more than other classes of individual (Wilcoxon signed ranks $T+ = 35$; $n = 9$; $p<0.2$, 2-tailed). This tendency wasn't significant because two mothers showed the opposite of this trend. Both mothers, Tita and Tanga, had only one small infant each, under the age of two. Grooming probably didn't have a social function because the infants were too young to reciprocate. When these two mothers were omitted from the analysis, then the effect was significant (Wilcoxon signed ranks $T+ = 28$; $n = 7$; $p < 0.05$, 2-tailed) showing that mothers

generally prefer to groom their offspring even when are members of the community are present. There was a very strong tendency for mothers to groom all their maternal relatives (both adult individuals and dependent offspring) significantly more than other individuals (Wilcoxon signed ranks T+ = 39; n = 9; p = 0.055, 2-tailed), suggesting that mothers are attracted to their maternal kin more than nonkin. After dependent offspring, Patti, Fifi, Gremlin and Fanni showed a preference to groom with adult relatives: Patti for her adult daughter Tanga, Fifi for her adult male sons, Fanni for her mother Fifi and Gremlin for her adult male brother. In contrast, Sandy groomed more with unrelated males than either her adult brother or her mother. Tita and Yolanda, immigrants with no known relatives in the community, also preferred to groom with adult males. Trezia, also an immigrant, showed no preference for males over females and only Tanga showed a preference for grooming unrelated adult females. The proportion of grooming time allocated to adult male relatives over male non-relatives was not significantly different (Wilcoxon signed ranks T+ = 6; n = 6; p >0.05, 2-tailed) and neither was the time allocated to adult female relatives compared to adult female non-relatives (Wilcoxon signed ranks T+ = 11; n = 5; p > 0.05, 2-tailed). Table 5 compares the amount of grooming directed to the average individual in each class for each mother. Although the time that each mother groomed with each male kin on average was not significantly different from that which she spent grooming with each nonkin male (Wilcoxon signed ranks T+ = 7; n = 4; p > 0.05, 2-tailed), there was a strong tendency for the proportion of grooming time allocated to each female kin on average, to be greater than the proportion allocated to the average female nonkin (Wilcoxon signed ranks T+ = 0; n = 5; p = 0.063,

2-tailed). This suggests that chimpanzee mothers show a strong social attraction to their female kin but not their male kin.

When I considered parties made up of non-maternally related individuals I found an age effect on grooming. There was a tendency for younger mothers, under the age of 21 to

mother	age	rank	Give to lower ranked females	Received from mothers(not kin)	Received from non mothers (not kin)	Received from average mother	Received from average nonmoth	Given to mothers (not kin)	Given to non-mothers(not kin)	Given to average mother(nonkin)	Given to average nonmother
Pi	40	1	0 039	0 062	0	0 062	0	0 011	0	0.011	0
ff	43	2	0 010	0	0.01	0	0 01	0	0	0	0
gm	31	3	0 029	0	0	0	0	0.07	0	0 018	0
sa	28	4	0 000	0	0	0	0	0	0	0	0
fn	20	5	0 051	0.011	0	0.011	0	0 07	0.004	0 018	0 004
tz	23	6	0 000	0 015	0.015	0.015	0 007	0 009	0	0 009	0
yd	15	7	0 000	0	0.055	0	0.028	0 014	0	0 014	0
tt	17	8	0 000	0 021	0 005	0.021	0 005	0 069	0	0.023	0
ta	12	9	0 000	0 17	0 117	0 084	0 039	0 003	0	0 003	0

Table 5: Shows the proportion of grooming in parties given to and received from various categories of individuals. Pi = Patti; ff = Fifi; gm = Gremlin; sa = Sandy; fn = Fanni; tz = Trezia; yd = Yolanda; tt = Tita; ta = Tanga. Rank 1 = highest rank, rank 9 = lowest.

spend a significantly greater proportion of their grooming time grooming both unrelated females (Mann-Whitney U = 3.00; n1 = 5 females over 21, n2 = 4 females under 21; p = 0.1, 2-tailed) and unrelated males (Mann-Whitney U = 3.00; n1 = 5 females over 21, n2 = 4 females under 21; p = 0.1, 2-tailed) than older mothers (see figure 11). Such an effect could have occurred however, not because younger females are intrinsically more social but because older females are constrained by a greater number of dependent offspring. Older females have a significantly greater number of dependent offspring than younger females (Mann-Whitney U = 1.50; n1 = 5, n2 = 4; $p < 0.05$, 2-tailed) and older females allocate a significantly larger proportion of their grooming budget to their offspring, in groups other than the family group (Mann-Whitney U = 0; n1 = 5; n2 = 4; $p < 0.05$, 2-tailed). While there was no significant difference between the two age classes in the proportion of grooming allocated to each offspring on average (Mann-Whitney U = 8.00; n1 = 5, n2 = 4; $p > 0.05$, 2-tailed), highly correlated was the number of offspring each

mother had and the proportion of her grooming budget allocated to them (Spearman's rho = 0.766; n = 9; $p < 0.05$, 2-tailed). This therefore suggests that mothers are constrained from grooming other adult members of the community by the number of dependent offspring they have, assuming that dependent offspring have the priority, at least when they are old enough to reciprocate. This may explain why females groom with other adults at lower rates than males. Rather than being intrinsically less social, mothers prioritise grooming with their dependent offspring and are thus constrained from grooming other member of their community, by them.

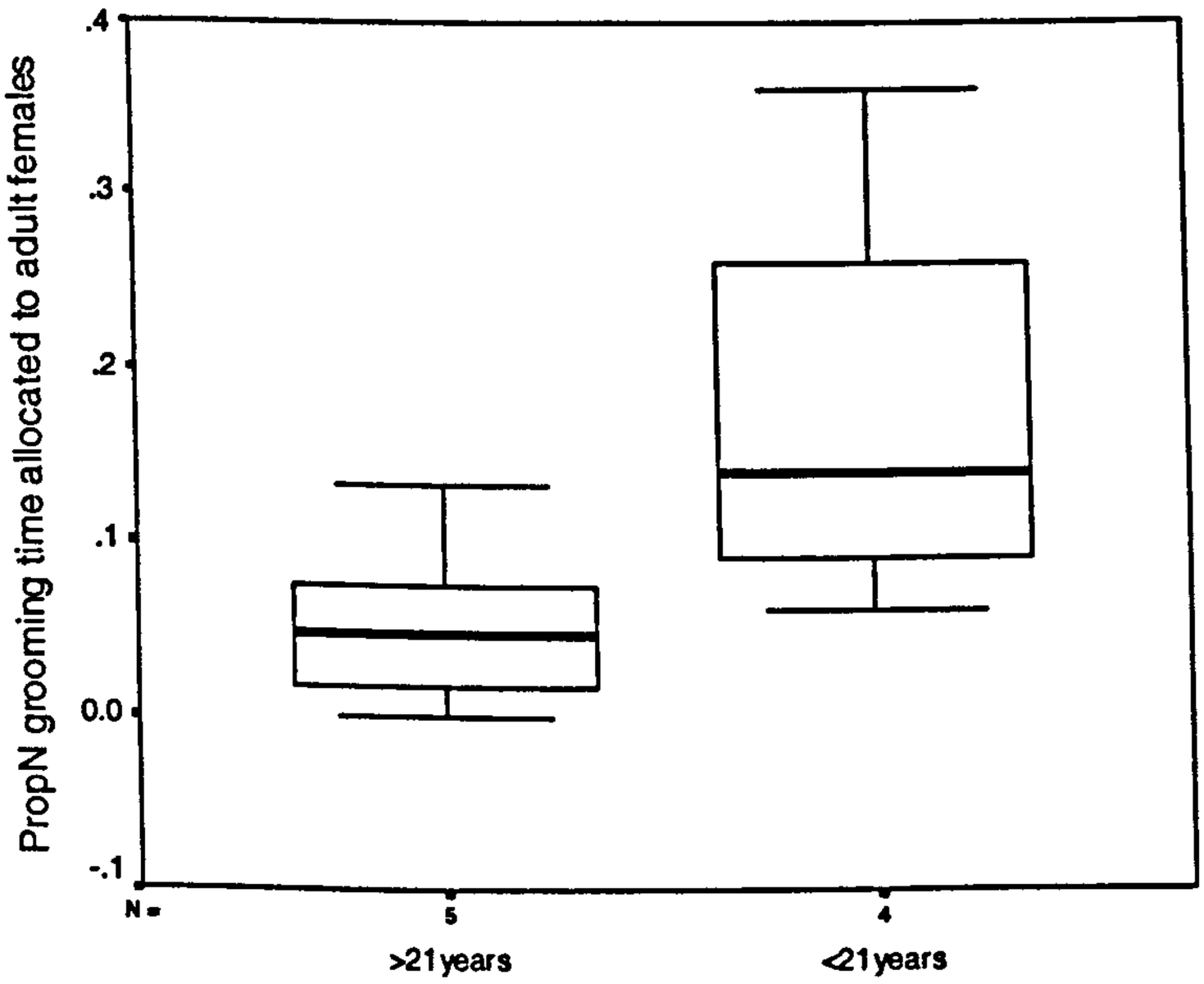


Figure 11: Box plot showing the proportion of grooming allocated to adult unrelated females for two age classes of mother. Each plot shows the median and quartiles within a category.

In order to investigate whether high-ranking females were more attractive grooming partners than lower-ranking females, I correlated the proportion of grooming received from other females with social rank (relative rank here) but found no significant effect (Spearman's rho = 0.1; n = 9; $p > 0.05$, 2-tailed). I did however find that females directed

a greater proportion of their grooming to higher-ranking females than lower ranking females (Wilcoxon signed ranks T+ = 2; n = 8; p< 0.05, 2-tailed), supporting the notion of attraction to high rank. However, when female kin were excluded from the analysis, this effect was no longer significant (Wilcoxon signed ranks T+ = 9; n = 9; p > 0.05, 2-tailed).

Mothers didn't receive significantly more grooming from female kin (Wilcoxon signed ranks T+ = 12; n = 6; p > 0.05, 2-tailed), even when grooming received from female adult kin on average was compared to that received from the average female nonkin (Wilcoxon signed rank T+ = 16; n = 6; p > 0.05, 2-tailed). There was however a tendency for mothers to give significantly more grooming to female kin on average than to the average nonkin (Wilcoxon signed ranks T+ = 19; n = 6; p < 0.1, 2-tailed) verifying a kin preference, although this effect was no longer significant when parties of maternally related individuals were omitted from the analysis, suggesting that this preference disappears in groups with maternally unrelated individuals.

I also compared the proportion of grooming received from and given to the average mother with that received from and given to the average female without dependent offspring. Although mothers did not receive on average more grooming from other mothers than from non-mothers (Wilcoxon signed ranks T+ = 21; n = 9; p > 0.05 2-tailed) they did direct a significantly greater proportion of their grooming on average to mothers than non-mothers (Wilcoxon signed ranks T+ = 0; n = 9; p < 0.05 2-tailed) and

this effect remained significant even when parties of maternally related individuals were omitted from the analysis suggesting an attraction between established females.

Summary

1. Mothers vary greatly in the amount of time they invest in grooming.

2. Mothers groomed with their dependent offspring who were old enough to reciprocate and all maternal relatives more than with other classes of individuals suggesting a greater attraction to kin over nonkin.

3. The proportion of time allocated to adult female kin on average was significantly greater than the proportion allocated to female nonkin on average. This relationship did not hold for adult male kin and nonkin suggesting that mothers show a stronger social attraction to their adult female kin over adult male kin.

4. Mothers directed more grooming to their adult female kin on average than adult female nonkin, to higher-ranking females on average than to lower-ranking females and to other mothers on average than females without dependent offspring. This suggests an attraction to high-ranking females, to kin and to established females.

5. Mothers did not receive more grooming from other mothers, from adult kin or from lower-ranking females suggesting that females are able to control how much grooming they give, but not how much grooming they receive from other individuals.

6. There was an age effect on grooming. Younger mothers, (<21) spent a significantly greater proportion of their grooming time grooming with unrelated adult males and females. This effect was due to the fact that mothers prioritise grooming with their offspring over other classes of individual and older females have a greater number of offspring leaving less time to groom with others.

2.4 Discussion

2.4.1 Dominance and the Female Hierarchy

The female dominance hierarchy at Gombe is strong, interactions are predictable and reversals were uncommon. Only two dyads showed reversals, in which an individual dominates another higher in rank (Appleby 1983). All others were unidirectional. Females acquired higher rank with age, marking one difference between the male and

female hierarchy; males attain high rank in their prime between about the ages of 20 and 25 years. This finding complements previous research on both the Gombe and Mahale populations (see Pusey, Williams & Goodall 1997) but runs contrary to findings from the Tai Forest population, Ivory Coast, where age and dominance rank did not correlate (Boesch & Boesch-Achermann 2000). Another difference is the level of stability within the ranks. The female hierarchy is more stable in time than the male hierarchy. If the female hierarchy was not stable and changed from year to year, as it does for males, then any benefits accrued while high-ranking would be off-set by disadvantages occurring when the same female is low ranking (Cote 2000). This is especially true for a slow reproducing species as the chimpanzee. Unlike some other species, where status among females appears dependent, to a degree, on age (e.g. mountain goat *Oreamnos americanus* Cote 2000), other factors other than the ability to survive, such as social ones, may play a part in attaining high rank. Patti for example was observed to challenge the alpha female Fifi in 1997 (personal observation, see Appendix two) when Fifi was ill and soon after acquired the alpha position. While the rank of a female at 21 years of age may be predictive of her rank ten years later (Pusey, Williams & Goodall 1997) other factors such as deaths and illnesses may serve to boost a female's status. Males often lose their alpha status as a result of ill health and subsequent challenges by lower-ranking males.

There were two main problems in assigning ranks to female chimpanzees, especially in terms of testing the degree of linearity. One involved the low frequency of interactions in general and the lack of interactions between some dyads, illustrated by zero values in the

dominance matrices. De Vries (1998) argued that some agonistic behavioural patterns are more suitable indicators of dominance, i.e. submissive behaviours by which one animal recognises and states its subordinate position. For chimpanzees, such behaviours: pant grunting, avoidance, and displacement occurred at too low a frequency to be used alone and more overt behaviours such as charge, displaying and fighting had to be included to rank the females. De Vries (1998) also presented a strong criterion for ranking individuals whereby the number of wins of one individual significantly differ from the wins observed by another before the first is called dominant to the second.

In assigning status scores using the Jameson, Appleby & Freeman (1999) method, I found that my data alone was insufficient to result in convergence but when I added just six more interactions from Gombe's long-term database, for the same period, convergence was achieved. This suggests that although 18 months may have been too short a period to gather enough data for some of the dyads, a longer period of perhaps 36 months would have been sufficient to have ranked most females, especially if they were the subjects of focal follows. For the nine mothers in the sample, it is doubtful that an extended data collection period would have resulted in a different order of rank. Focal sampling of these females produced the most dyadic interactions and almost certainly most if not all parous females with dependent offspring are higher ranking than either the nulliparous females or the few parous females without dependent offspring, although there are rare exceptions (e.g. Gigi, Pusey, *personal communication*). The combination of methods followed did however result in a hierarchy that matched well to my own observations and impressions.

Another limitation of all three methods was the assumption that the hierarchy had to be linear or near linear in nature. Testing for linearity is complicated by a large number of unknown dominance relationships. According to de Vries (1995) the type of unknown relationship has different consequences for the way the linearity in a set of dominance relationships should be statistically tested (de Vries 1995). De Vries differentiated between dyads that could in principle show agonistic interactions but are never observed to do so and those for which it is structurally impossible to show agonistic interactions and a dominance relationship is absent. Although unknown relationships, between some females in this study, may have occurred because interactions were never observed, the possibility remains that due to the nature of chimpanzee society some dyads do not have a dominance relationship, especially dyads involving a new nulliparous female immigrant who might choose to avoid interactions with more established females.

The presence of intransitive triads indicates that the hierarchy is non-linear. In order for the female hierarchy to be linear female chimpanzees would have to monitor not just their relationships with other community members but also others' relationships with community members. Since females live in a fission fusion society and spend a large proportion of their time foraging solitarily with their dependent offspring, this appears an impossible undertaking. Some dyads associated regularly, especially those sharing the same neighbourhood (Williams *et al.* 2002) but other dyads, i.e. those from different neighbourhoods were never seen to interact and only met in large mixed groups where the presence of males appeared to depress interactions between females. This is possible since observations on a wide range of nonhuman primates have shown that in a variety of

contexts, the presence of the opposite sex can inhibit the expression of some behaviours that are released in their absence (see Smuts 1987). It may be unimportant for female chimpanzees to keep track of all their relationships; if females are competing for rich food sources then it is especially important for females, who share a common neighbourhood and overlapping ranges, to maintain unambiguous relationships at least at the dyadic level. Beacham (2003) demonstrated that prior experience was probably a more important determinant of linearity than intrinsic factors such as size and a lack of interactions between some female chimpanzees and a lack of stable matrilines across all females, may explain this lack of linearity. In circumstances where smaller individuals avoid larger ones, avoidance can have significant effects on the degree of sequential relationship formation within component triads of a group, causing individuals with similar resource holding potential to be in closer proximity and increasing the chances of sequential relationship development among these subset of individuals (Beacham 2003), resulting in transitive triads. Alternatively, Beacham (2003) found that if an intrinsic factor such as body size, alone, determines hierarchy rank, linearity is not to be expected.

The results of this study reveal that age is a major determining factor of female rank in chimpanzees and higher-ranking females have higher body weight (Pusey, Williams & Oerlert, unpublished data in Williams, Liu & Pusey 2002). The non-linearity of the female dominance hierarchy could be caused either because the fission-fusion nature of chimpanzee society results in partially solitary females with some females (e.g. nulliparous immigrants) avoiding others (e.g. parous residents), or because status is determined solely by age. Interestingly, however, the only two dyads showing reversals, in which an individual appeared to dominate another higher in rank consisted of a

mother-adult daughter pair, Fifi and her daughter Fanni, (Fifi pant-grunted to Fanni) and two close associates, Gremlin and Tanga (Tanga charged, unprovoked, at Gremlin). Certainly, the mechanism behind the female dominance hierarchy requires further research but despite the difficulties in assigning rank, I believe that the results presented still provide a useful insight into the dominance structure of the female chimpanzees at Gombe, using existing analytical tools.

2.4.2 Rank, Energy Consumption and Female Philopatry

Results suggest that high- ranking females and their adult daughters who remain in the natal community consume higher energy diets than lower ranking females. Better nutrition may therefore account for several aspects of greater reproductive success in high-ranking females at Gombe (Pusey, Williams & Goodall 1997). The fact that these females consume a higher proportion of fruit in their diet but spend no greater time feeding, suggests that they consume better quality food at higher rates and are more efficient feeders in terms of energy uptake. Admittedly, rate of fruit consumption is an indirect measure of nutrient acquisition and a broadly defined condition (Gore 1993) but measuring absolute rates is confounded by observational difficulties in the field and the caloric value of different food items remains unknown.

As a consequence, the unusually high proportion of females who do not transfer at Gombe, 50% (Pusey, Williams & Goodall 1997), may have an incentive to stay. Van Schaik (1989) proposed that as a consequence of increased contest competition the incentives for emigration and transfer should be small and hence, female dominance and

female philopatry often occur together. Where within-group scramble competition exists female reproductive success is directly influenced by group density and as this increases so should the degree of scramble competition and the inclination for females to leave. The costs of emigration and transfer should also be smaller since a female should neither experience the disadvantages associated with being at the bottom of a hierarchy or overt aggression.

Despite the fact that external factors, such as the degradation of the habitat and decrease in numbers of adult males of the two neighbouring communities in the Park, may have, in recent times, made emigration a less attractive strategy, this high rate of female philopatry has always been the case (Pusey *personal communication*) at least in the forty years since research began. Therefore differences between this population and others do not appear to reflect non-adaptive situations caused by recent human induced ecological changes (Sterck, Watts & van Schaik 1997), although this point remains debateable, especially since such human-induced ecological changes have arguably been occurring at Gombe for almost as long as the long-term research study. Certainly habitat degradation, in proximity to the official park boundaries, has contributed to the decrease in numbers of the other two communities in the Park (effectively destroying significant proportions of their respective community ranges) and females are possibly more likely to remain in large than small communities (Nishida & Hiraiwa-Hasegawa 1987) where they can secure more food and be reproductively more successful (Williams *et al.* 2004). Since adult daughters appear to have similar ranges to their mothers, and it should pay for mothers according to kin selection theory to tolerate their kin more than unrelated

females as neighbours, high-ranking mothers and their adult daughters may defend core areas containing higher quality food than other females. This appears likely due to the mosaic distribution of vegetation at Gombe. The high proportion of aggressive and dominance interactions between females that were supported by kin also points to another benefit derived from female philopatry. Support from female kin, also reflected in the grooming data, may be more common than from male kin. Although the number of interactions supported by female kin was not significantly greater than that from male kin, all interactions involving the support of male kin involved just one family (Fifi's). All mothers with adult female kin were however observed to support each other. In the Arnhem chimpanzee colony, in the Netherlands, adult male coalitions are, to a certain degree, independent of previously existing social bonds, in contrast to the largely bond-dependent interventions of adult females (de Waal 1987). These benefits may outweigh the multiple costs of transferring; costs in aggression received from resident females, costs in entering at the bottom of the hierarchy and energetic costs in initially ranging in sub-optimal habitat and having to learn the whereabouts of new sources of food. The fact that female chimpanzees normally only transfer once, at Gombe, compared to other populations and other primate species which transfer multiple times (Sterck 1997), suggests that transferring is a costly strategy for chimpanzees at Gombe. This is supported by evidence from Williams *et al.* (2002). It appears likely, therefore, that the degree of contest competition and the size and condition of neighbouring communities may affect the dispersal patterns of Gombe chimpanzees more than factors associated with within-group scramble competition because females increase their reproductive success in larger groups (Williams *et al.* 2004), in direct contrast to the predictions of

scramble competition. While van Schaik (1989) predicted that the combination of strong within-group competition and female dispersal should be extremely rare, only occurring if a factor other than food exerts an overriding selective pressure toward female dispersal (van Schaik 1989), it is possible that the relative number of males in neighbouring communities may drive females to disperse under certain conditions; such as that experienced presently in the Kalande community where a decrease in the number of adult males to one, has led to an influx of females into the Kasekela community.

In turn, the higher rates of aggression between females, at Gombe, can be viewed as a product of female philopatry and the evolution of kin support between females. This is best illustrated by a comparison of female social relationships reported by Boesch & Boesch-Achermann (2000), at their field site in Tai Forest, Ivory Coast, where it is claimed that the social structure resembles more that of bonobos *Pan paniscus*. Here, all adolescent females transfer and resident females are not aggressive to new immigrants. Furthermore females do not appear to have clear-cut home ranges and are reported to be more social, spending more time in groups, suggesting that within-group contest competition is not as intense as at Gombe. This may be reflected in the finding that the age of first parturition among females is about equal among females (Boesch & Boesch-Achermann 2000), whereas that at Gombe appears far more varied. In this population, tolerance from resident males appears more important than from resident females, in the context of competition with females. In contrast, new immigrants associate almost constantly with males, and have a lengthy cycling period before conception, with swellings viewed as "social passports" for tolerance. As a result of the greater cohesion

between the sexes, Tai chimpanzees spend more of their time in mixed parties. Mothers support their sons actively in social life (Boesch & Boesch-Achermann 2000), signifying that between populations, kin-support is utilised flexibly as a product of different dispersal patterns and the degree of relatedness between classes of individual.

At Gombe, young females, even daughters of high-ranking females, do often temporarily emigrate suggesting that females may actively weigh up the costs and benefits of transfer before deciding on a community in which to reproduce. One other determining factor of female transfer may be the presence of an older sister in the natal community. Whereas Fanni, Fifi's oldest daughter, remained in the Kasekela community, her second daughter transferred to the northern Mitumba community, suggesting that benefits of being the daughter of a high ranking female may, because of the costs associated with feeding competition only extend to the one daughter. This daughter inherits the parental social environment (Getty & Capaldi 1994) as well as parental genes and in doing so has a high chance of acquiring high rank; these may be the emerging patterns. Both Fifi and Pom temporarily transferred before returning to their natal community and both had high-ranking mothers (Pusey 1983) while the only female to do so at Mahale was the daughter of the second highest –ranking female (Nishida 1979 in Pusey 1983). Such social dynamics, governing dispersal patterns, have been found in a wide range of species. Emlen (1984, in Emlen 1998) showed that yearling acorn woodpeckers *Melanerpes formicivorus*, among other examples of bird species, had a decreased tendency to disperse with decreasing availability of breeding vacancies and offspring from high-quality

territories were less likely to disperse since dispersal to even higher-quality territories was less likely (Stacey & Ligon 1987, in Emlen 1998).

2.4.3 Female Sociability

Mothers who consumed higher energy diets also spent more time in parties and results suggested that, since females consume more fruit while foraging alone, these mothers could afford the lower foraging rates in parties, while costs were higher for other mothers who were lower in rank or who did not have a high-ranking mother. The proportion of time spent in a party therefore appeared largely determined by nutrient acquisition. Whereas all females socialised with males at similar rates, female-female associations appeared far more differentiated due to the effects of contest competition (see Williams, Liu & Pusey 2002). Mother-daughter pairs, not surprisingly, associated the most together but mothers also preferred to associate with other mothers more than other females, supporting Williams, Liu & Pusey (2002) who found that established resident females preferred to associate together more than with immigrants. Such an effect could also be a product of rank on sociability because similarly ranked females prefer to associate together (Williams, Liu & Pusey 2002), since low ranking females associating with higher ranking females would incur significant costs associated with contest over defendable food resources. Although rank was not established for all females, in this study it is probable that the females without dependent offspring were lower ranking, in most cases, than all mothers sampled. Mothers who socialised the most with other mothers also socialised more with non-mothers and mothers who were more social with females were also more social with males. A mother's sociability with females was

correlated to the proportion of time she spent in parties whereas a mother's sociability with males was not, perhaps because females predominated in the groups that mothers joined. Good relationships among females and their relative competitive abilities may be crucial factors determining whether females join groups, particularly because competition among females tends to be low-key but chronic (Smuts 1987). What is clear is that differentiation of female-female association patterns, not apparent in the female-male association patterns, suggests that relationships among females are extremely influential in the social structure of the community.

2.4.4 Female Grooming Patterns

Because female chimpanzees groom rarely compared to that between males, is has received scant attention resulting in the impression that it is rather unimportant. Results suggest that females groom less than males because they are constrained by the number of dependent offspring they have. Mothers prioritise their dependent offspring for grooming, possibly for ecto-parasite removal and as an investment for future support and while there was large variation in the time spent grooming across all mothers, unrelated to rank, suggesting that grooming per se isn't a costly behaviour, the proportion of grooming allocated to offspring was positively correlated to the number of offspring. Lee (1983) suggested that where there are energetic costs attached to interactions, such as conditions of seasonal or relatively low food availability, there are benefits of concentrating relationships among kin. Younger mothers were subsequently able to groom unrelated adult members of the community at higher rates than older females because they were freed from the time consuming act of grooming several dependent

offspring. This is in accordance with Seyfarth (1977) who recognised that the number of a female's offspring is one social factor, which sets an upper limit on the time, which individuals can attempt to spend, interacting with other adult females (Seyfarth 1977) and may aid young females in their establishment of relationships as breeding females with status.

Grooming is associated with alliances (e.g. Hemelrijk 1994) and the results suggest that grooming among females flows between kin and from subordinates to dominants as expected if grooming aids in the maintenance of coalitions (Seyfarth 1977, in Wrangham 1980) and is exchanged for feeding tolerance (Payne *et al.* 2003). Mothers groomed with adult female relatives, on average, at significantly higher rates than they groomed with adult male relatives, suggesting a strong attraction to adult female kin but not to adult male kin. This complements findings by Pusey (1978 in Pusey 1983) who demonstrated a tendency, at Gombe, for sons to groom their mothers less than daughters, in proportion to the amount that mothers groomed them and contrasts with the finding of a higher overall degree of grooming reciprocity in the Tai population (Boesch & Boesch-Achermann 2000), where female-female bonds are less defined. Mothers gave more grooming to their adult female kin than to adult female nonkin but did not receive more. Mothers also directed significantly more grooming to higher-ranking females than to lower-ranking females but did not receive significantly more grooming from lower ranking females, supporting the notion of a social attraction to higher-ranking females. This effect disappeared when adult female kin were controlled for so interpretation of rank effects may also be attributed to kinship. However mothers gave significantly more grooming to

other mothers than to females without dependent offspring and this effect remained significant even when adult female kin were controlled for, suggesting an attraction to established higher-ranking mothers among established mothers. Despite the confounding effects of rank and kin the results do support de Waal & Luttrell's (1986) "similarity principle" in which individuals are attracted to others similar to themselves. This they suggested as an adaptive strategy because coalitions made up of similar individuals offered greater probability of compatibility.

While the results supports Seyfarth's model (1977) that females have goals in terms of particular grooming partners, with grooming patterns being nepotistic and rank related, the results run contrary to the model concerning the distribution of grooming given and received between any two individuals. Seyfarth's model was, however, at least partially based upon the grooming patterns of just four primate species, all with linear female dominance hierarchies. Seyfarth assumed that receiving grooming would always bring benefits at a higher rate than giving, so females will attempt to receive more grooming than they give. This assumption rested on the fact that while grooming given will bring benefit according to the rank of one's partner (Seyfarth 1977) (a social benefit), grooming received will bring about the same benefit plus a benefit in the removal of ectoparasites. Equal weight appears to have been given to each of these benefits while the relative importance of each has yet to be quantified. While grooming may have initially evolved to function in the removal of ectoparasites, it is also possible that its social function may have evolved in importance, so that presently, its function is not that which it was originally selected for. For instance, although chimpanzees can intensely groom a

specific area on either their of their associate's body, and appear to be removing something, I have never observed the removal of visible ectoparasites and it remains a puzzling phenomenon to observers. Could chimpanzees be "pretending" to provide a service, in order to reap social benefits at a later date? Indeed, in a later paper, Seyfarth was unable to show that the primary function of grooming, among vervets, was the removal of ectoparasites (Seyfarth 1980).

Grooming relations between female monkeys, under Seyfarth's model, can be explained in terms of competition for and the attractiveness of high-ranking females. Results in Seyfarth's study of six groups of monkeys, comprising three species, in free-range or captive conditions, rhesus macaque *m. mulatta,* gelada baboon *t. gelada,* chacma baboon *p.c. ursinus*, showed that high-ranking females received more grooming than lower-ranking females but there was no relationship between rank and grooming given.

Reasons why chimpanzee-grooming networks have dissimilar features to some other monkey species may also lie in differences in aspects of social structure. Because chimpanzee society is of a fission-fusion nature and females are largely solitary, and at Gombe appear to live in two distinct neighbourhoods (see Williams *et al.* 2002), competition for grooming partners may not be so intense as in species with more permanent grouping patterns and the decision of whom to groom may rely more upon who is present at any particular point in time. Rather than low-ranking females being constrained from grooming higher-ranking females by females higher in rank than them, possibly more influential constraints are imposed on all females by their solitary nature

and the temporal and spatial distribution of potential grooming partners. The fact that female chimpanzees are able to control the amount of grooming given but not the amount of grooming received and therefore fulfil their grooming objectives (e.g. Heinzi *et al.* 2003) could be a consequence of partial solitary living, i.e. its within the control of females to choose to preferentially groom the higher-ranking females whom they meet, but not how much they receive in relation to their rank, since this will depend upon the frequency with which they meet lower-ranking females.

Hemelrijk (1994) showed that for the long-tailed macaque M*acaca fascicularis,* a species of monkey which under natural conditions also lives in a fission-fusion society, females supported others more after being groomed by them in the recent past than without prior grooming, but a female who received grooming from another individual did not receive more support from that individual more often than without foregoing grooming. This suggests that there are tangible benefits to giving grooming over receiving it, running contrary to Seyfarth's model, at least for species living in fission-fusion societies and high-ranking females may be more predisposed to support their associates.

2.4.5 Food Distribution and Female Social Organisation: Gombe versus Budongo

The difference in female social organisation, recorded between sites, is probably due to differences in food availability, defined as the combination of the amount/abundance and the spatial arrangement/dispersion of food within a given location at a specified time (Newton-Fisher, Reynolds & Plumptre 2000). At Budongo, and for the Sonso community of chimpanzees, several factors suggest that food availability may be higher than for the

Kasekela community at Gombe. The community home range size at Sonso has been estimated at 7 kilometre squared (Newton-Fisher 2003) which is far smaller than at other sites with comparative numbers, including Gombe, and the Sonso chimpanzees therefore live at much higher densities. Although Williams *et al.* (2002) estimated the Kasekela community at Gombe to have had a minimum range size of about 5 kilometres squared, the range size has fluctuated quite widely; during 1975-1978 community range size was 12 kilometres squared and presently it is much greater than any prior period. Home range size is likely to be indicative of resource availability with low abundance and high dispersal of food resources combining to produce larger ranges (Newton-Fisher 2003). Data from Sonso suggests that there is a local abundance of resources, since the large number of males present does not imply that the community is forced into a small range due to pressure from surrounding communities. Furthermore, females at Sonso do not appear to maintain core areas or neighbourhoods, suggesting that either there is not the "room" to do so, or contest competition is less important. Unlike Gombe, which has the most similar diet (Newton-Fisher 1999), figs are a major food source comprising 36% of the diet (Emery, *personal communication*) and are considered a staple food source, being consumed year-round. Food scarcity is not apparent (Newton-Fisher 1999). Subjective impressions of the size of fig trees in these two sites, suggest that fig trees at Budongo are larger and the diameter at breast height of the source tree is a good predictor of fruit abundance (Chapman *et al.* 1992 in Newton-Fisher, Reynolds & Plumptre 2000). Newton-Fisher, Reynolds & Plumptre (2000) showed that at Sonso there was a weak relationship between food availability and the size of chimp parties suggesting that other factors, particularly social ones such as the number of swollen (cycling) females, were

responsible for group size. They went on to propose a curvilinear model of the relationship between food abundance and party size in which the constraints of a limited food supply became weakened as abundance increased until food supply became unimportant in determining the size of parties (Newton-Fisher, Reynolds & Plumptre 2000).

At Gombe females maintain discrete core areas (Williams *et al.* 2002) and parous females with offspring spend approximately 40% of their time alone in their core areas with their dependent offspring (Pusey, Williams & Goodall 1997). The prevalence of pant-grunting among the female chimpanzees at Gombe may therefore be the product of both high within-group competition resulting in differentiated relationships and the need to formalise these relationships again after a period of solitary foraging, not observed in some other sites (e.g. Tai Forest, Boesch & Boesch-Achermann 2000). Along with other behavioural indicators, such as higher rates of aggression and infanticide by females, the presence of discrete core areas suggests that competition for space and food is higher at Gombe than at other sites. Van Schaik (1989) suggested the possibility that changes in the distribution of food would have different consequences on different populations, and used a comparison of two langur (*Presbytis entellus*) populations as an example (Jay 1965; Hardy 1977; Sugiyama 1967 all in van Schaik 1989). Mitchell, Boinski & van Schaik (1991), comparing two species of squirrel monkey *Samiri oerstedi* and *samiri sciureus,* proposed that differences in patch selection was due to differences in the distribution of available patches between sites, resulting in competitive regimes that produced a markedly different social structure. Scramble competition among female

chimpanzees at Budongo and at Tai, for instance, may be a more important factor for these populations, resulting in a more egalitarian hierarchy. These are indicators, therefore, that there may be a greater degree of variation in female primate relationships between different populations than between males. What is clear from this study is that relationships among female chimpanzees at Gombe are differentiated, as is expected in primate species with high within-group contest competition. The data supports the view that the hierarchy is reflected in the patterning of affiliative relationships (Payne *et al.* 2003). Grooming is directed up the hierarchy and between kin and kin and close associates support the majority of aggressive interactions. Sociability among females, driven by the demands of feeding competition, is somewhere intermediary between individualistic and nepotistic, rank-related and a crucial component of chimpanzee society at Gombe.

3 Do Mothers Influence the Sociability of their Offspring?

3.1 Introduction

3.1.1 Hypothesis to Test

Chapter two investigated rank and kin effects on the distribution of grooming and association patterns among female chimpanzees, in particular mothers, at Gombe. I showed that the female chimpanzees at Gombe order themselves into a stable, consistent and despotic hierarchy, and that the effects of high rank on reproductive success (Pusey, Williams & Goodall 1997) and sociability were probably due to increased energy uptake by high-ranking females. Both the female dominance hierarchy and the high degree of female philopatry expressed at Gombe were adaptations to high within-group contest competition. As a result of this, relationships among females were highly differentiated, with mothers showing strong attraction to both kin and high-ranking females.

In this chapter I investigate how certain characteristics of the mother affect her ability to provide her offspring opportunities for social play by examining the following hypothesis:

Ha = The sociability of a mother has a direct effect on the sociability of her offspring.

Ho = The sociability of a mother has no effect on the sociability of her offspring.

In particular I want to investigate how mothers influence the sociability of their offspring.

Two particular but interrelated questions that I am interested in are:

1. Do the associations between mothers determine the associations of their offspring?

2. Will offspring form stable social networks and what determines these networks?

3.1.2 Predictions from Current Knowledge

For chimpanzees living in fission-fusion societies where party membership changes frequently, the only long-term party is a mother with her dependent offspring (Nishida & Hiraiwa-Hasegawa 1987). Because the mother coordinates travel and which parties to join, she may determine the social milieu of her offspring more than mothers of other species who live in permanent social groups. If there are large differences in the social experiences of mothers then these should also translate across to their offspring. If high-ranking mothers and their adult daughters secure richer diets and are able to afford the costs of grouping, this suggests that their dependent offspring will spend a greater proportion of their time in social groups. Mothers who show strong preferences to socialise with other mothers provide social opportunities for their offspring. In turn, this might suggest that the consequences of feeding competition impacts, not only a female's reproductive success directly but also indirectly through the social development of her offspring. If maternal associations determine the associations of offspring then offspring may socially interact more with kin than non-kin and thus function as members of their lineage from the very beginning (Berman 1982), as has been found in some other primate species (e.g. rhesus macaques *Macaca mulatta,* Berman 1982) but not in all (e.g. yellow

baboon *Papio cynocephalus,* Altmann 2001). Similarly, offspring may interact more with offspring whose mothers are closely ranked to their own, since females of similar rank associate most together (Williams, Liu & Pusey 2002). If such patterns persist then this suggests long-term consequences of certain aspects of a mother's sociability on the development of her offspring's.

3.1.3 Social Play: Networks and Most Frequent Partners

In order to investigate this hypothesis, I investigate play behaviour. Specifically, I investigate how different aspects of a mother's sociability, her degree of relatedness to other members of the community, her length of residency in the community and her diet affect the play behaviour of her offspring. Consequently, the social networks alluded to in this chapter are specifically social play networks based upon most frequent play partners. For chimpanzees, little is known about how the social characteristics and experiences of a mother and the presence of siblings influence the social development of offspring. Because in many non-human primates dependent offspring play more frequently with their sibling than other animals of their sibling's age and sex, the availability of siblings will clearly affect the distribution of play partners (Cheney 1978).

Analysis was limited to social play for a number of reasons. First, play is a conspicuous behaviour. Second, it is the most frequent social behaviour observed between dependent offspring and is almost exclusively observed between juveniles, being transient in many mammalian species (Burghardt 1998). Third, research on play behaviour has been plagued with difficulties in the assignment of definitions and functional explanations.

Therefore the study of play behaviour may allow for strong insights into its function. Specifically I look at social play, which is performed at much higher frequencies than other forms of play (see Table 1). As children's play frequently reflects their degree of liking for each other (Boulton 1991 in Thompson 1998), I assume that the frequency of play between chimpanzee dependent offspring, although possibly reflecting the association patterns of mothers, also or as a consequence, reflects the degree of liking among dependent offspring. If specific types and amounts of play experience are necessary for optimal development, then natural selection should favour individuals who select play partners that best fulfil these requirements (Thompson 1996). The fact that play in chimpanzees is primarily social may be indicative of its prime function and the examination of most frequent play-partners and sex differences may provide critical information about the adaptive significance of social play (Fagen 1981). While it could be argued that focusing on one category of play reduces the ability to understand the diversity of play, this study focuses on social play in order to understand its evolved social function, which is assumed to be relatively important in such a socially complex species as the chimpanzee (e.g. Smith 1982). This chapter seeks to investigate how social relationships are developed during the period when offspring are still dependent upon their mothers, a lengthy period spanning more or less the first decade of life.

3.1.4 Findings

In this chapter I produce results suggesting that social play frequencies are determined by the diet quality of the individual and his/her mother. I show that social mothers produce offspring who play at higher rates. I also show that dependent offspring play most

frequently with just a few play partners, and social play frequencies between dyads are determined by both the mothers' relative ranks, maternal relatedness, and ultimately the degree to which mothers associate together. I present one sex difference in social play frequencies that may have adaptive significance in later life and with my findings support the "social cohesion" function of play. Importantly the social lives of females at Gombe appear distinct in many ways to the social lives of females in other populations and research findings will therefore be discussed in light of this at the end of the chapter.

3.2 Methods

3.2.1 Study Population and Field Methods

Data were collected on the habituated Kasekela community of chimpanzees at Gombe National Park, in Tanzania, from July 2001 until March 2002 and again from June 2002 until March 2003. Data on thirteen dependent offspring of six parous females were collected during the first fieldwork period (see appendix one). This was then expanded to seventeen dependent offspring in the second fieldwork period, when three more family groups were added to the sample. In total, 30 hours of data were collected on all offspring followed during both field work periods and 15 hours of data were collected on all offspring that were followed during just the second field work period. Although sample size appears small, the sample encompassed 90% of the total number of family groups in the community, at that time. Dependent offspring were defined as all chimpanzees that had not yet reached maturity, and maintained close association with the mother and family group. Maturity is defined as the age at which females first give birth and raise an

offspring, or in the case of males, full adult body size is reached and full integration into the society of adult males is achieved (Goodall 1986). During normal development, offspring maintain close association with their mothers until after they reach puberty and adolescence, at between the ages of 10-12 years of age. All except one individual was clearly defined in this way. One male in the sample, ten-year old Ferdinand, associated less and less with his mother and dependent sibling during the course of the study. While at the start of the study, he showed obvious signs of distress when he lost his mother, half way through, he appeared virtually independent of his mother, although he had by no means gained body mass appropriate to a young adult male, by the end of the study.

The age of all offspring, and their relationships with other members of the community, were known from long-term records. I classed offspring as infants, juveniles or adolescents following Goodall's definitions. Goodall (1986) defined infancy from zero to five years, the juvenile period from five to seven years and adolescence from eight to ten years in females and eight to twelve years in males. The oldest adolescent in the sample was an eleven year old female, who was nonetheless considered an adolescent due to the high level of association she had with her mother and the fact that she only started to show adult sized sexual swellings at the end of the study when data collection on her was completed. Although Goodall's definitions act as a good guide, there is a lot of inter-individual variation in the timing of these life phases. A three to four year old, whose mother has given birth early to another infant, would be classed as a juvenile, since weaning would almost be complete, she would not be consuming her mother's milk and she would be expected to travel by herself. Gardner-Roberts (1998) redefined infancy

from zero to three and a half years, after which offspring are less dependent upon their mothers for travel and travel mainly by themselves, i.e. they don't rely on their mothers to carry them. This redefinition has been used quite extensively in recent papers (e.g. Williams, Liu & Pusey 2002). In this chapter, since sample size was small, I defined infancy from zero to five years. However, since the older infants in this study were far more advanced, developmentally, than the youngest and were therefore not truly comparable to them, I also define independently travelling infants as those infants who by the middle of the study were travelling extensively by themselves. This represented a sub-group whose daily energy expenditure was considered most similar and therefore enabled fairer comparisons.

Data was collected using focal animal sampling techniques (Altmann 1974). Follows on dependent offspring varied in length but 86% were over 2 hours in length, a minimum advised by Robert Hinde when he helped design the mother-infant long-term research at Gombe during the 1960s. The longest follow was 9.5 hours, and 25% of follows were over 5 hours in length. Mothers and their dependent offspring were normally followed from morning until nesting time in the evening. Missing data fell within recommended levels (below 10%). Missing data comprised 14% of the data collected from one dependent offspring who was especially hard to follow. However, overall, missing values were not thought to bias analysis and data was therefore not corrected. Follows were rotated so that all females were sampled at systematic intervals. Systematic data collection was hard to maintain since three of the nine family groups were not well habituated and therefore were followed opportunistically when they were observed.

However, two out of these three families did tolerate lone follows with humans. The other family appeared completely unbothered by humans while in a group, but showed little or no tolerance towards humans when alone. While there was a compromise between collecting strict systematic data and collecting sufficient data on all family groups, there was a conscious effort to follow individuals equally between the morning and the afternoon and while in groups of different composition. Hence, only one family group did not tolerate humans while foraging alone, and was therefore over-sampled while in larger parties.

General data on and changes in group/party membership, including the identification of cycling females, were collected along with the sexual state of the target's mother (normally non-cycling and lactating except in two cases), the weather, the approximate location of the target (valley and gully name) and the vegetation type according to Clutton-Brocks's (1972; in Goodall 1986) five major types. Data were recorded as these variables changed. Only in very large mixed groups, where it was hard to keep track of changing group membership, were individuals present recorded just at the start and the end of the follow. The general behaviour of dependent offspring recorded, differed slightly depending on whether the individual was an infant, a juvenile or an adolescent. For all dependent offspring, data were collected every minute, and proximity to the mother and sibling(s) were recorded as either touching, within arm's reach, within 5 metres, further than 5 metres and further than 15 metres. General behaviour of the target was recorded every minute and in addition, for infants, the general behaviour of the mother was also recorded. When the target was feeding, the species of food and the part

consumed (e.g. leaf, fruit, flower) was recorded. General behaviour provided the context in which comparatively rare behaviours such as play occurred. The context was defined as the behaviour that was occurring prior to play, or in the case of infants, the mother's behaviour prior to the onset of playing. This was useful because infants spent relatively little time in behaviours such as feeding or were just harder to observe due to their smaller size, so recording just the infant's behaviour was not always sufficient to gauge the behaviour of the rest of the group. The activity budgets of older dependent offspring appeared more synchronised with that of the mother.

Play behaviour of the target was recorded when it was observed regardless of whether it occurred on or off the minute. Social play sessions were recorded on mini-DV, using a Sony digital video camera recorder (DCR-TRV15E). Participants of a play session were recorded as playing either at the start or sometime during each minute of play, depending on when they joined. Where possible, the identification of the individual who initiated and/or terminated the session was made. However initiations and terminations were very hard to record with confidence from direct observation, since often, for example, the apparent initiator appeared to be responding to subtle cues from another participant. These cues were possibly facial expressions, which were hard to observe. Terminations were harder to record as often participants appeared to mutually terminate the session together.

3.2.2 Measures and Definitions

Diet quality was defined as the proportion of total focal time feeding that was spent feeding on fruit and palm nuts. Although this is a rough measure of diet quality, since the caloric value of each food item remains unknown, it was assumed that both fruit and palm nuts represented energy rich foods. Other food types, such as leaves and flowers, were assumed to have very little energy value. Some food items such as termites and meat were assumed to be highly nutritious, but because they were consumed comparatively rarely and were representative of totally different food sources, they were not included, since it could not be assumed that they were directly comparable to fruit and palm nuts, in terms of the rate of energy intake. Time spent feeding was defined as the proportion of total focal time spent feeding.

Party types were recorded based upon definitions provided by Goodall (1986). For this analysis parties were defined as either family, nursery or mixed. Goodall defines family groups comprised of a mother and her dependents, with or without older offspring; nursery groups comprised of two or more family units sometimes accompanied by unrelated childless females; and mixed groups comprised of one or more adult or adolescent males with one or more adult or adolescent females, with or without dependent offspring. In this analysis I defined a family group accompanied by adult offspring as mixed (if adult is male) or nursery (if adult is female with her own offspring). Rather than base group definitions on degree of relatedness, I chose to base them on ecological and social factors. A mother who associates with her adult daughter and dependent offspring is associating within a nursery group and will have the same

ecological constraints imposed upon her as when she is associating in other similar sized groups, regardless of the degree of relatedness.

Maternal behaviours relevant to this chapter, such as *general gregariousness,* the *dyadic association index, relative rank* and *grooming frequencies*, are defined in detail in chapter two.

Social play was defined as any "playful" behaviour involving both the target and at least one other individual, responding in a "playful" way to the actions of the other. Social lay comprised both rough and tumble (R&T) wrestling and chasing. Table 1 shows the overall social play frequencies of target individuals, which include social play with both immature and adult members of the community. Social play with adults, including mothers, was however, rare. *Overall social play frequencies* were defined as a count of the number of minutes where social play of the target was observed, expressed as a proportion of total focal time followed (in minutes) in groups with other dependent offspring, which constituted the vast majority of play partners. These included bouts/sessions that lasted for less than one minute. Although some of these could be classed as failed initiations, most bouts/sessions lasting less than one minute provoked another individual to respond in a playful way. For individuals with dependent siblings this was analogous to total time followed as the focal, since these individuals were always in the presence of other dependent offspring. For offspring without dependent siblings, this corresponded to the time in which they were followed in groups other than the family group. Defining play frequencies in this way controlled to some extent for the

fact that individuals with dependent siblings have more opportunity to play. *A play session* was defined as play behaviour that was not interrupted by more than two minutes, whereby the play partners engaged in another activity or rested. Bouts, a string of which are considered a session, could not be defined from direct observation, in part because play in chimpanzees is so varied and in part because definitions of bouts are unsatisfactory, at least when applied to chimpanzee play. *Most frequent play partner* was defined in terms of a count of the minutes in which the target was observed to play with specific individuals as a proportion of the count of total focal minutes in which the target was observed to play socially. Since play with adults was so rare, analysis concentrated on play with other dependent offspring.

Only offspring who spent the majority of their focal time followed in groups other than family groups were considered in the subsequent analyses. Ferdinand, an adolescent and the oldest male in the study sample, was omitted since his low social play rate was a consequence of his age, characterised by spending most of his time establishing associations with adult males and spending little time with his mother and dependent siblings. In previous years he had participated in play sequences frequently. Tom was also omitted, and his low rate of play was attributed to the fact that 70% of the time that he was the focal; he was travelling alone with his mother who had no other offspring. The proportion of focal time he spent playing did not therefore appear representative of the true proportion of time he spent socially playing.

3.2.3 Analysis

Statistical analysis was performed using the SPSS statistical package. Due to small sample sizes, non-parametric tests were used. Correlations were tested with Spearman's rho. The Mann-Whitney U test and the Wilcoxon paired ranks test were utilised in analyses involving two independent and dependent groups, respectively. All statistical tests were two tailed, with an exact significance threshold of 0.05. Non-significant tendencies were defined as tests that yielded a significance threshold of less than 0.1.

ID	Age	Mother	rela. Rank mother	focal mins followed	% time in groups	% time in social play	% time in lone/object
tzn	2.25	Patti (PI)	1	2851	89	14.42	9.96
tn	7.75	Patti (PI)	1	2560	94	12.23	1.13
flr	3.75	Fifi (FF)	2	2818	95	15.79	2.45
fe	10.00	Fifi (FF)	2	1428			
ga	9.25	Gremlin (GM)	3	2202	100	4.81	1.54
gld	3.75	Gremlin (GM)	3	3023	100	10.98	5.29
glt	3.75	Gremlin (GM)	3	2568	100	8.02	3.04
sr	11.25	Sandy (SA)	4	2311	98	1.47	0.04
sm	6.00	Sandy (SA)	4	2466	100	5.35	1.09
sam	1.00	Sandy (SA)	4	1105	100	7.6	3.61
fu	5.50	Fanni (FN)	5	2957	100	15.96	2.4
fun	2.00	Fanni (FN)	5	2495	100	15.03	6.13
zs	7.50	Trezia (TZ)	6	1183	99	15.05	0.169
zla	2.50	Trezia (TZ)	6	1317	94	10.78	2.58
yam	3.50	Yolanda (YD)	7	1341	79	4.62	0.67
tof	1.50	Tita (TT)	8	620	67	9.35	9.8
tom	1.25	Tanga (TA)	9	1335	36		

Table 1: first column identifies the dependent offspring in the sample(tzn = Tarzan, tn = Titan, flr = Flirt, Fe = Ferdinand, ga = Gaia, gld = Golden, glt = Glitter, sr = Sherehe, sm = Samson, sam = Samantha, fu = Fudge, fun = Fundi, zs = Zeus, zla = Zella, yam = Yamaha, tof = Tofiki, tom = Tom); age of each dependent offspring half way through data collection; mother's identity; relative rank of mother; the total number of minutes followed during the fieldwork period; the percentage of total focal time spent playing; the percentage of focal time spent in groups other than the family group; the percentage of focal time in social play with all age classes of individual, determined as a count of the number of minutes playing with at least one other individual as a proportion of total time followed; the percentage of time spent in lone or object play.

3.3 Results

3.3.1 Ecological Determinants of Play

I first investigated whether a mother's diet quality, defined as the proportion of her diet made up of fruit and palm nuts, was correlated with the social play frequencies of her offspring. Figure 1 shows a scatter plot of the percentage of fruit in a mother's diet against the percentage time her offspring spent in social play. The percentage time spent in social play was significantly correlated to the mother's diet quality (Spearman's rho = 0.846; n = 15; $p < 0.01$, 2-tailed). Offspring of mothers who ate higher energy diets

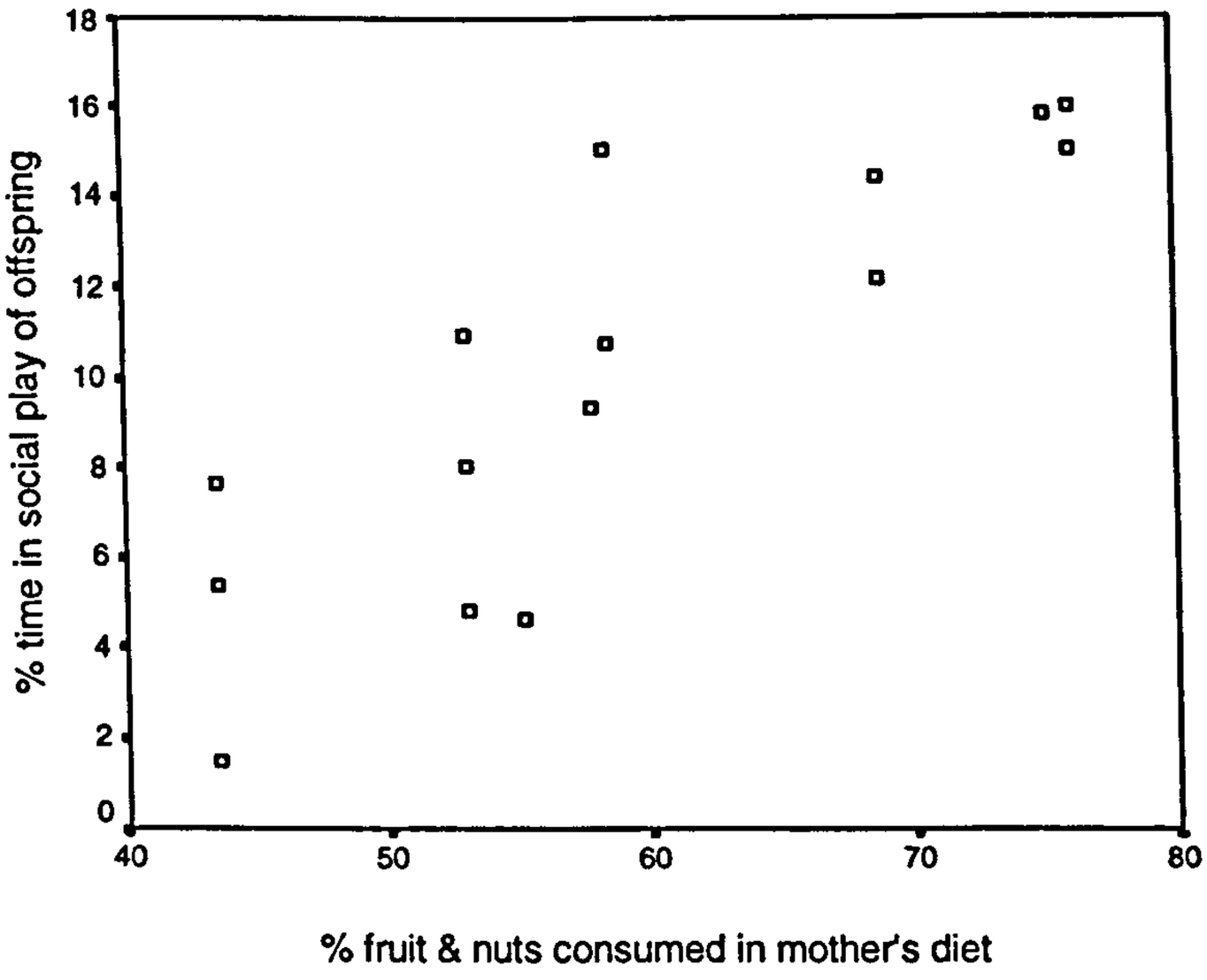


Figure 1: Scatter plot showing the social play frequencies of 15 dependent offspring of various ages against the diet quality of their respective mothers, defined as the proportion of fruit and palm nuts consumed in their diets.

played at higher frequencies than the offspring of mothers with lower energy diets. Figure 2 shows a box plot representing the difference in play frequencies between dependent offspring of high-ranking females and their adult daughters who had not permanently transferred as adults and other mothers. Offspring of these high-ranking females and their

adult daughters socially played at significantly higher frequencies than the offspring of other females (Mann-Whitney U = 3.00; n1 = 5; n2 = 10; p <0.01, 2-tailed).

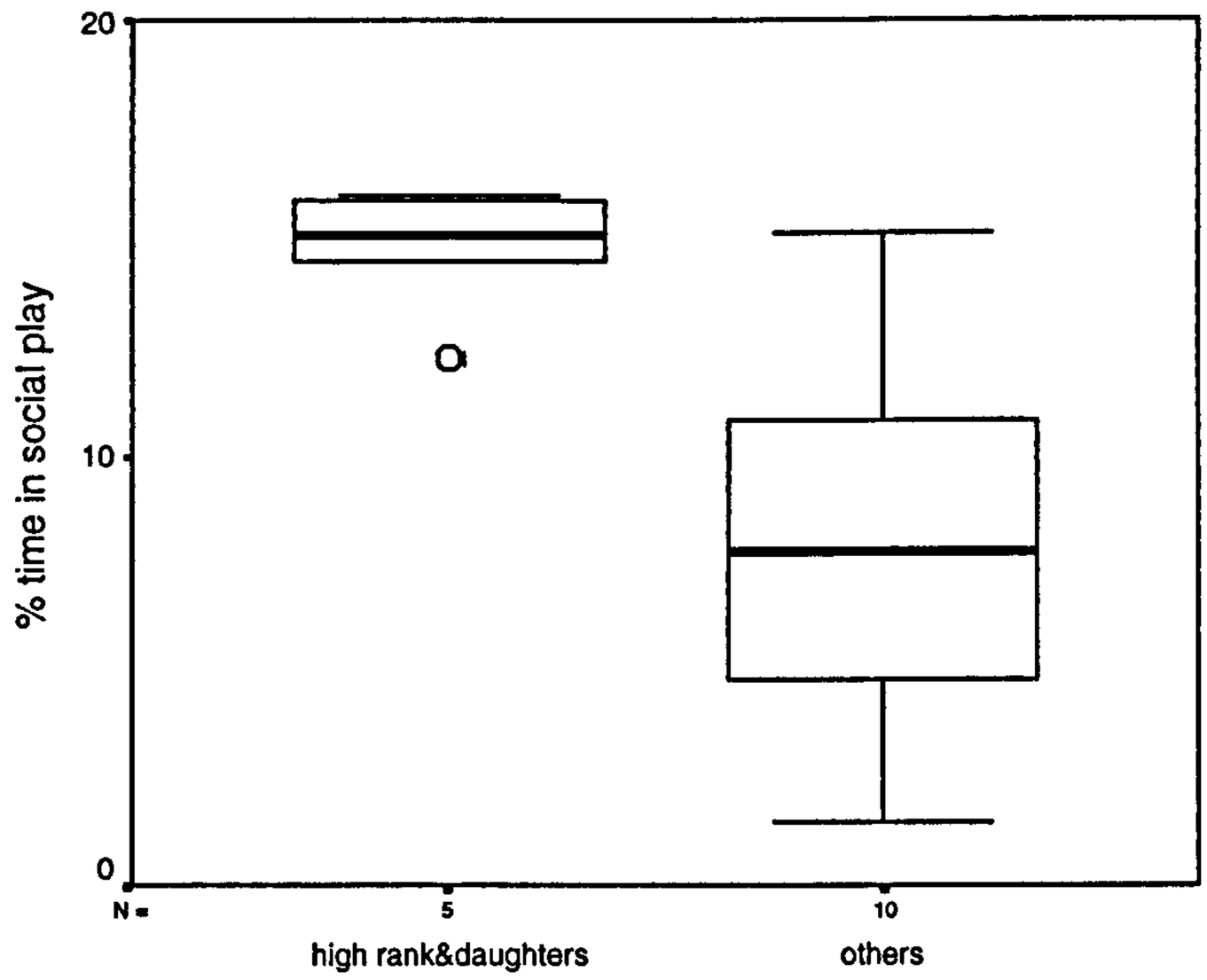


Figure 2: Box plot showing the difference in social play frequency between the offspring of high-ranking females and their adult daughters and the dependent offspring of all other mothers. Each plot shows the median, quartiles and outliers within a category.

Since older mothers have significantly more dependent offspring (see chapter two) these results may be due to the fact that the offspring of high-ranking females just have more dependent siblings to play with more of the time. I investigated this by comparing social play frequencies of dependent offspring with individuals other than family members (mother and dependent siblings), in groups other than family groups. This is comparable to a measure of offspring sociability with unrelated individuals. Figure 3 shows a scatter plot of the linear relationship between a mother's diet quality and the frequency with which her offspring played with individuals other than those in their immediate family. There was a significant correlation between the diet quality of the mother and the frequency with which her offspring played socially (Spearman's rho = 0.707; n = 15; p < 0.01, 2-tailed). Mothers who ate higher quality diets, in terms of proportion of fruit and

palm nuts consumed, produced offspring who were more playful and more social towards individuals outside the immediate family. Furthermore, and as a consequence, the dependent offspring of high-ranking females and their adult daughters socially played at significantly higher frequencies with non-immediate family members than the offspring of other mothers (Mann-Whitney U = 8.00; n = 15; p <0.05, 2-tailed).

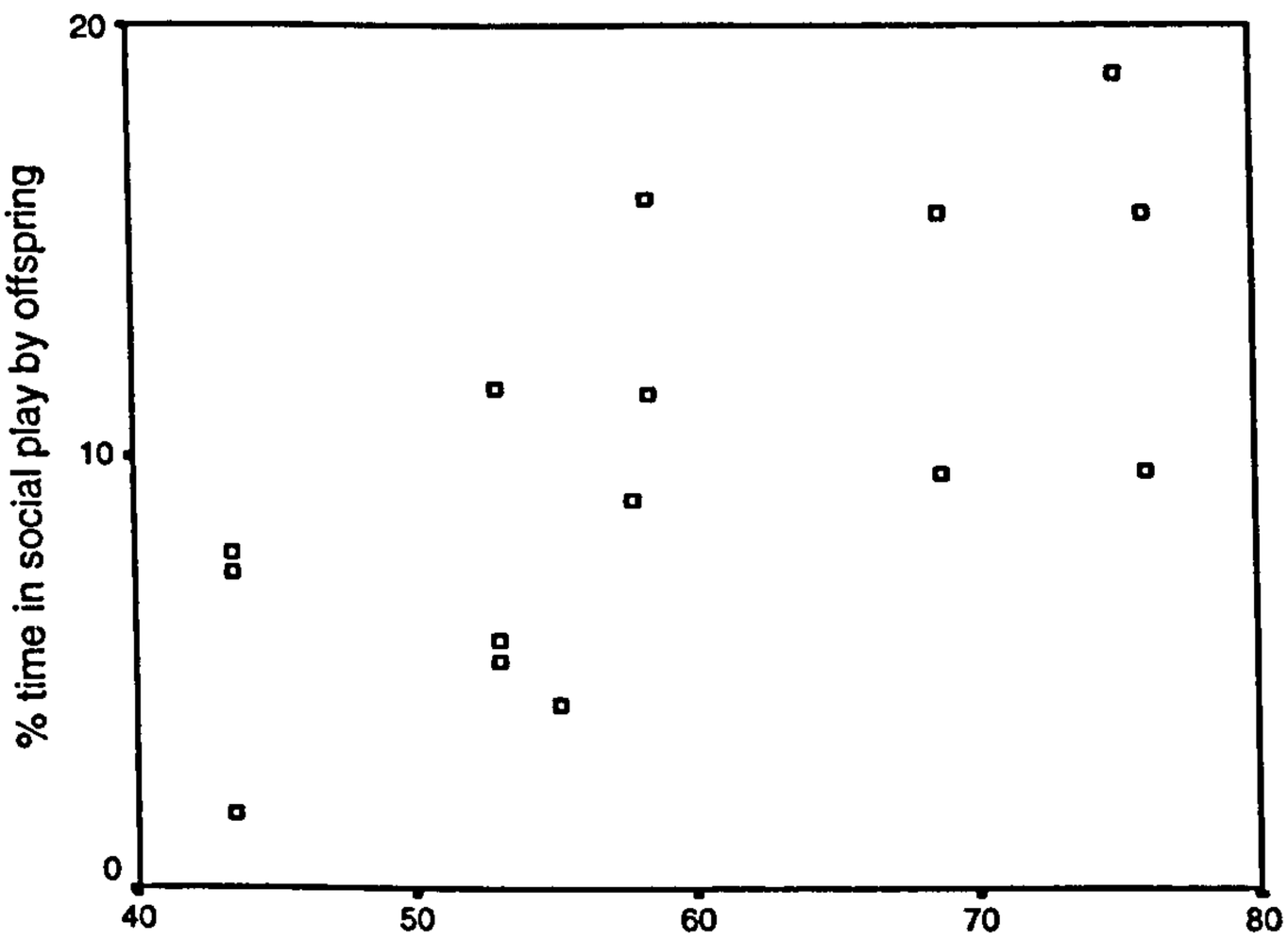


Figure 3: Scatter plot showing the relationship between the diet quality of the mother and the frequency of her dependent offspring's social play with individuals outside the family group (in all groups except family groups).

Diet quality of dependent offspring, defined as the proportion of fruit consumed in the diet, was not correlated to the age of dependent offspring (Spearman's rho = -3.05; n = 15; p>0.05, 2-tailed) and overall social play frequency was also not correlated to the age of dependent offspring (Spearman's rho = - 0.093; n = 15; p>0.05, 2-tailed). Since data collected on all target dependent offspring did not occur as systematically as hoped, due to the difficulties in finding particular family groups at specific times, sources of inter-individual differences on social play frequencies may have been biased by random sampling errors, if some dependent offspring were over- or under-sampled during peak

versus non-peak play times. To investigate this I first sought evidence for peak play times during the day. Social play rates across the day are shown in figure 4.

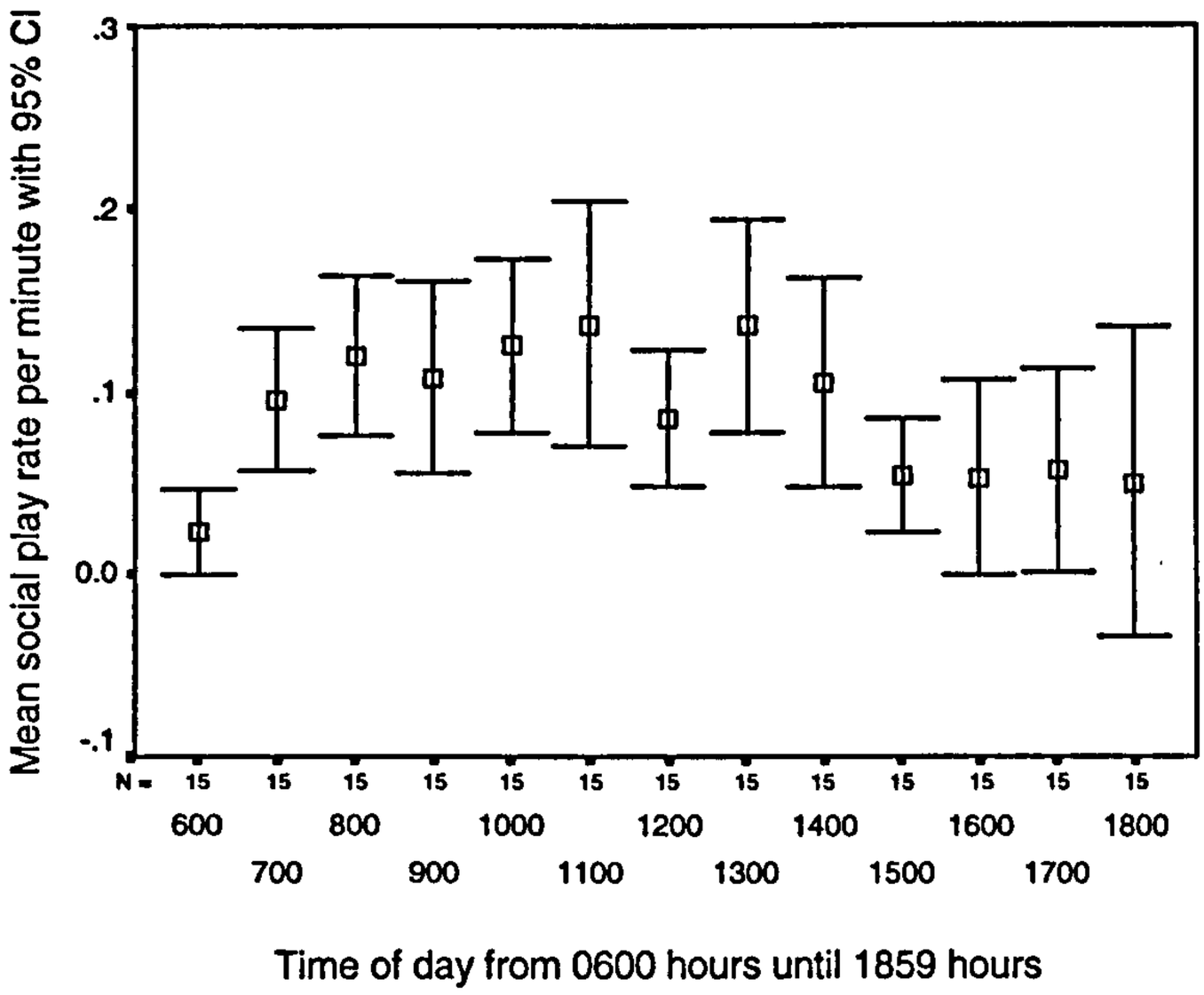


Figure 4: Mean rates of social play across all dependent offspring sampled, for each hour of the day, with 95% confidence intervals.

Figure 4 shows little evidence for peak play times. The means shown are tightly distributed and all but one of the confidence intervals overlap, suggesting that no play peaks occur consistently over all individuals. Therefore differences in the distribution of observations are highly unlikely to bias social play rates since play occurs at fairly constant rates throughout the day.

Since, for example, very young infants consume most of their energy through suckling and are biased towards eating soft fruit, proportion of fruit consumed in the diet doesn't give a fair estimate of energy consumption and comparison across age classes is misleading. I therefore investigated two age groups separately: juveniles and independently travelling infants. Figure 5 shows a scatter plot of social play frequency

against percentage of fruit consumed in the diet, for four juveniles. Individuals were classed as juveniles if they were between five and eight years of age in the middle of the study. The correlation coefficient was high, suggesting a relationship between social play frequency and the proportion of fruit in the diet. However, the coefficient didn't reach significance probably because the sample size was small (Spearman's rho = 0.8; n = 4; p>0.05, 2-tailed). There was a strong tendency, though, for juveniles and adolescents who spent less time feeding to spend a greater amount of time in social play (Spearman's rho = -0.771; n = 6; p = 0.072, 2-tailed), suggesting that the level of play could be related to the abundance and quality of food resources. A comparison of play rates between the wet and the dry season was not investigated due to the assumed high variance of food abundance within each season.

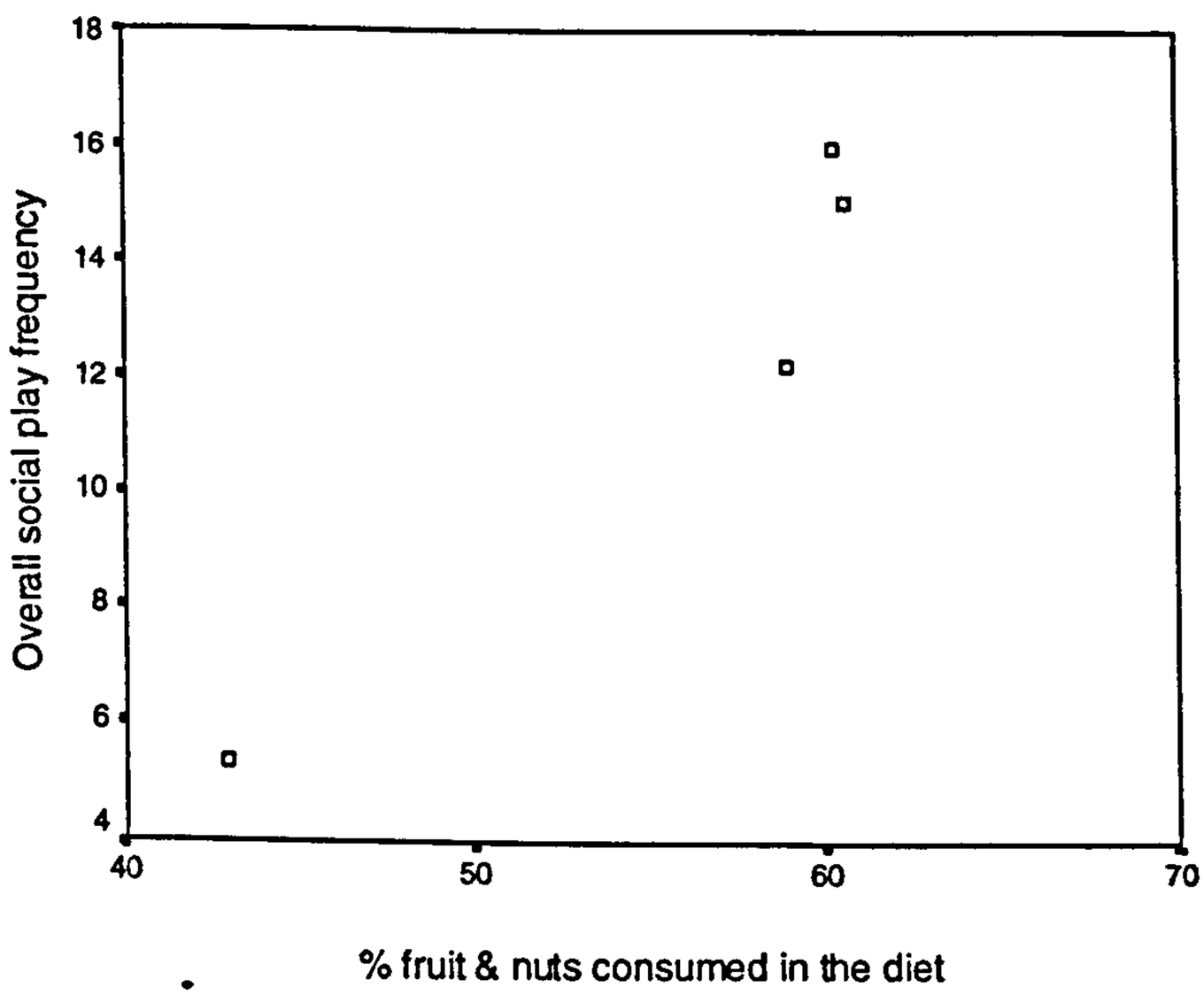


Figure 5: Scatter plot showing overall social play frequencies against the percentage of fruit and palm nuts consumed in the diet for four juvenile offspring.

Figure 6 shows a scatter plot of diet quality, for five independently travelling infants, against overall social play frequency. These included infants under the age of five years,

who were still suckling but who tended to travel independently of their mother, most of the time, by the middle of the study. There was a significant and positive correlation between overall social play frequency and the proportion of fruit and palm nuts consumed in the diet (Spearman's rho = 0.9; n = 5; $p<0.05$, 2-tailed). Independently travelling infants who consumed higher energy diets, played at higher frequencies than infants who consumed a smaller proportion of fruit and palm nuts. However there was no significant relationship between time spent feeding and time spent in social play (Spearman's rho = 0.3; n = 5; $p>0.05$, 2-tailed).

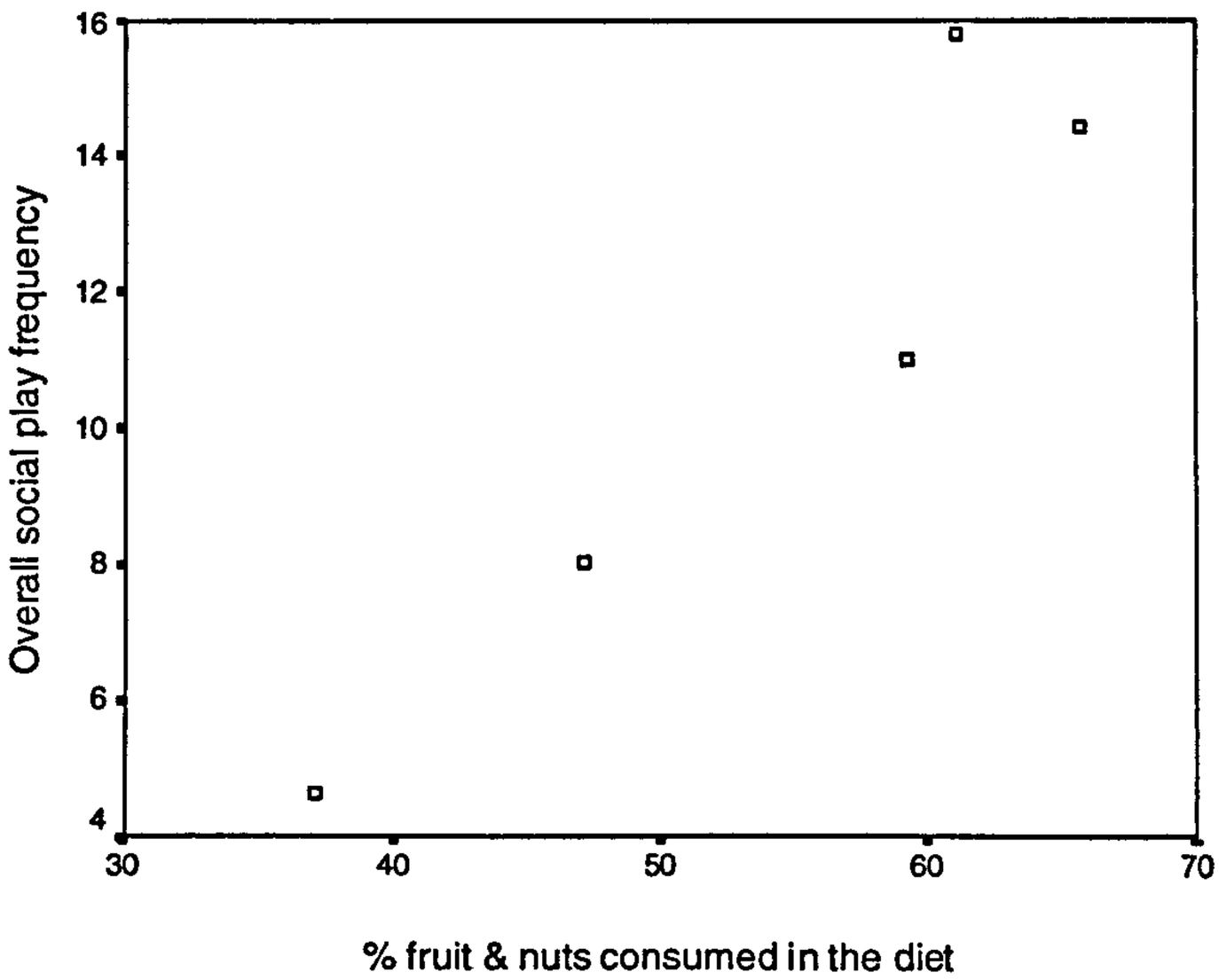


Figure 6: Scatter plot showing the overall social play frequencies of independently travelling infants against their diet quality, expressed as the percentage of fruit and palm nuts consumed in the diet.

An ecological determinant of social play is diet quality. At Gombe there are large differences in terms of the energy consumed by different females, which consequently may affect the energy consumed by their dependent offspring. Figure 7 shows a scatter plot comparing the consumption of fruit by mothers and their dependent offspring. The proportion of fruit consumed in dependent offspring's diet was not correlated to that

consumed by the mother (Spearman's rho = 0.156; n = 17; p>0.05, 2-tailed). Even when fruit consumption of the mothers was compared with that consumed by different age groups of offspring, (for independently travelling offspring Spearman's rho = 0.564; n = 5; p>0.05, 2-tailed; and for juveniles/early adolescents Spearman's rho = 0.345; n = 7; p>0.05, 2-tailed), no linear relationship was found. This is a surprising result because one

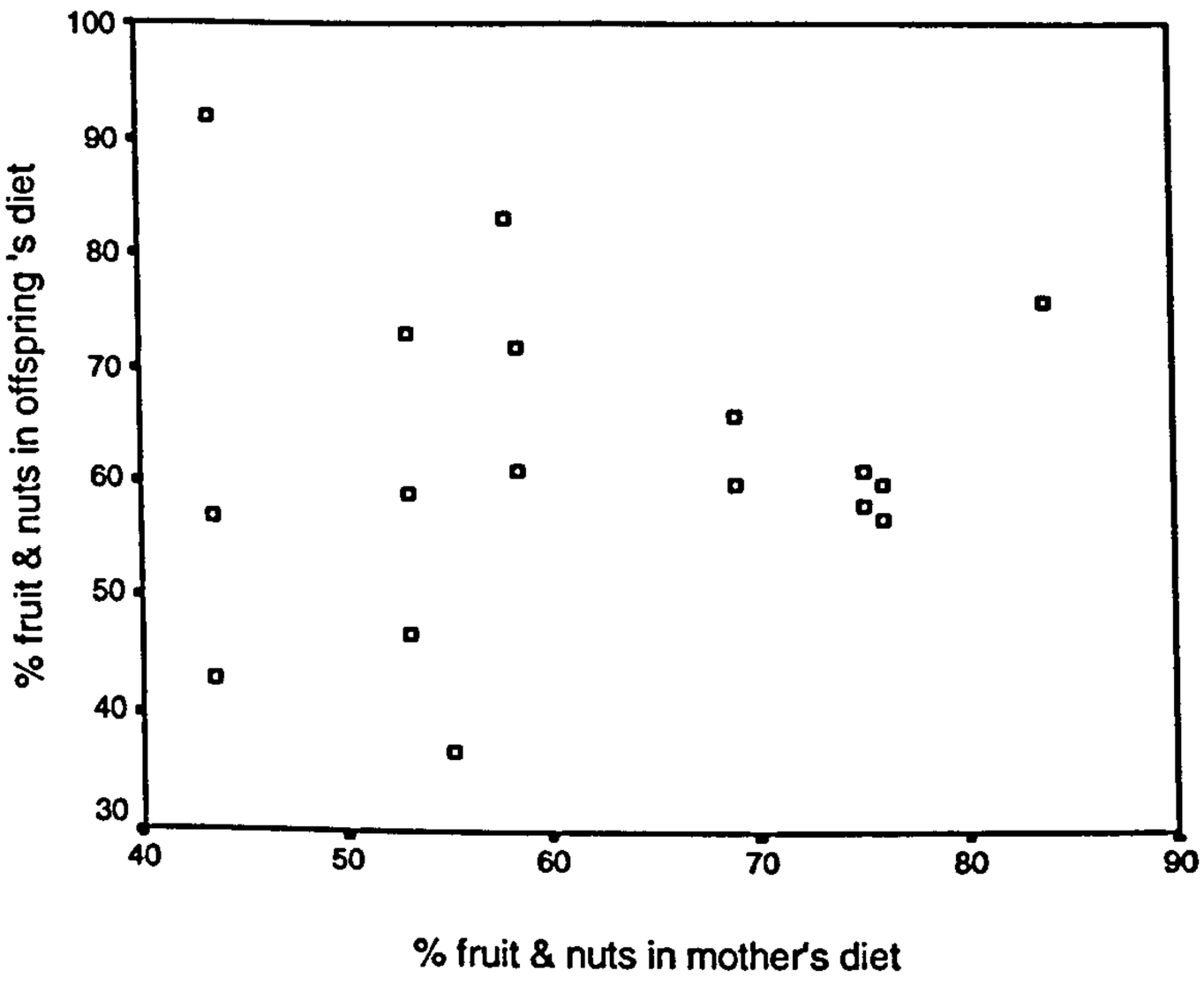


Figure 7: Scatter plot comparing mother's diet with that of her offspring.

would expect that a mother's ability to secure high energy food sources for herself would have a direct effect on the energy consumed by her offspring, with mothers who consumed higher quality diets producing offspring who did likewise. Assuming that there are benefits to social play, dependent offspring with high-ranking relatives have a social advantage; they are more playful and social than the offspring of other mothers. The proportion of focal time spent in social play was not correlated to the proportion of time spent resting for either independently travelling infants (Spearman's rho = -0.5; n = 5; p>0.05, 2-tailed), or juveniles and adolescents (Spearman's rho = 0.314; n = 6; p>0.05, 2-

tailed), suggesting that rates of social play were independent of the general activity levels of the subjects.

3.3.2 Social Determinants of Play

I also investigated the effect of group composition on play frequencies. Figure 8 compares the rate of social play among dependent offspring between groups where the dependent sibling was the only potential immature playmate and groups where other dependent offspring were present. Offspring played at significantly higher rates in groups where other dependent offspring were present than in groups where the dependent sibling was the only potential immature playmate (Wilcoxon signed ranks $T+ = 91$; $n = 13$; $p<0.01$, 2-tailed). This might suggest that dependent offspring are attracted to play with less familiar individuals, those individuals who are not encountered all of the time and suggests that one possible function of grouping for mothers might be the socialisation of their dependent offspring and play among dependent offspring may serve to re-establish relationships after a period of absence.

For all dependent offspring, overall social play frequencies were computed for within family groups, nursery groups and mixed groups. Sexual groups, sexual gatherings and gatherings (see Goodall 1986) were all lumped as mixed groups. Frequencies of overall social play differed significantly between groups for all offspring (Friedman chi- squared = 15.6; df = 2; $p<0.01$, 2-tailed). The mean rank scores for each group type showed that offspring played at much lower rates in family groups than in either nursery or mixed groups (mean rank: mixed = 2.20; nursery = 2.60; family = 1.20). To investigate whether

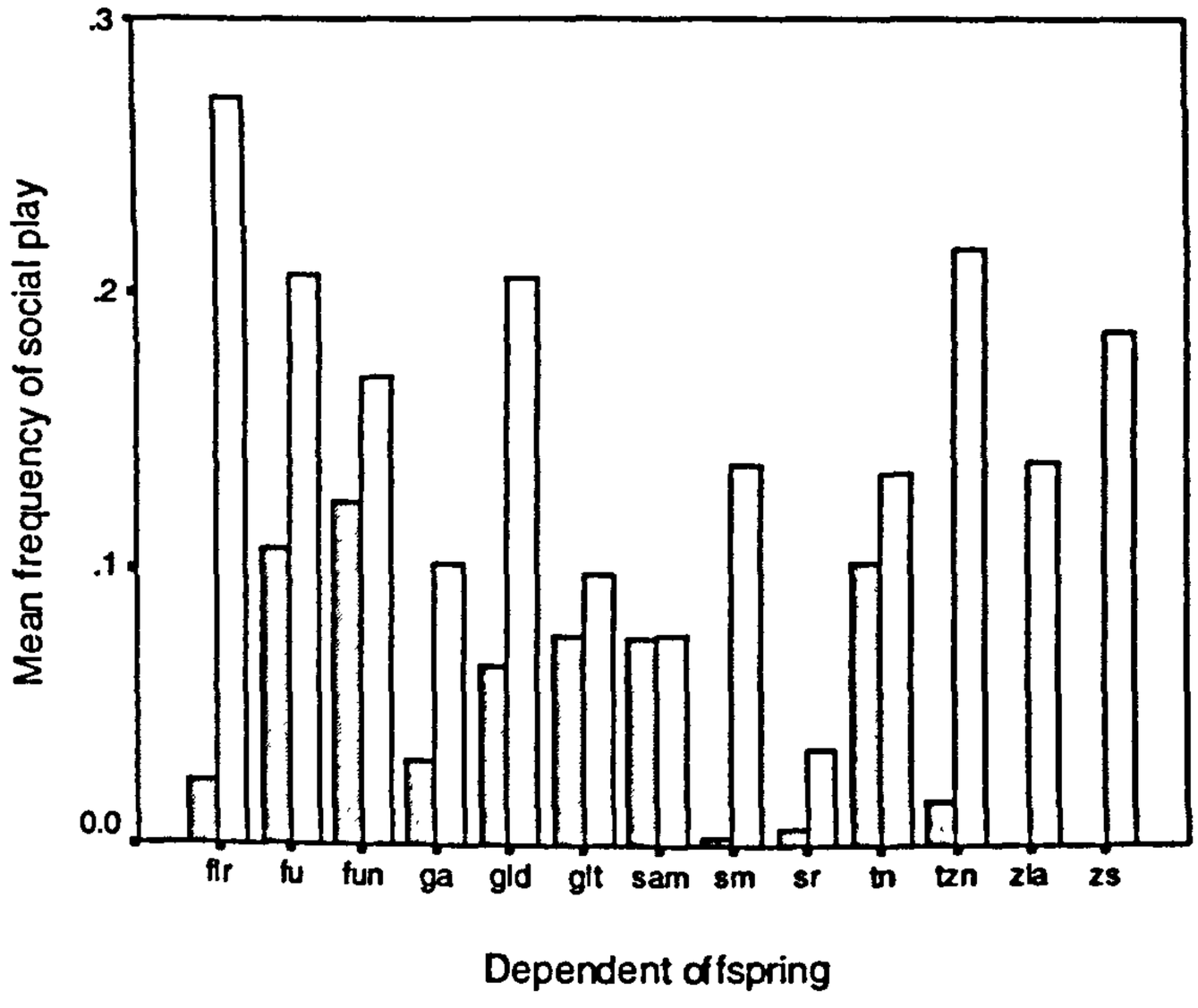


Figure 8: Bar chart comparing rates of social play in groups where the dependent sibling is the only potential immature playmate (filled columns) and groups where other dependent offspring are present (unfilled columns).

there was a significant difference in the frequencies of overall social play in nursery and mixed groups I analysed two groups of dependent offspring separately: infants and juveniles/adolescents (see figures 9 and 10). Infants played significantly more in nursery groups than in mixed groups (Wilcoxon signed ranks $T+ = 33$; $n = 8$; $p<0.05$, 2-tailed) but juveniles and adolescents did not (Wilcoxon signed ranks $T+ = 19$; $n = 7$; $p>0.05$, 2-tailed). This therefore supports the theory that nursery groups are safer social environments for infants to play in.

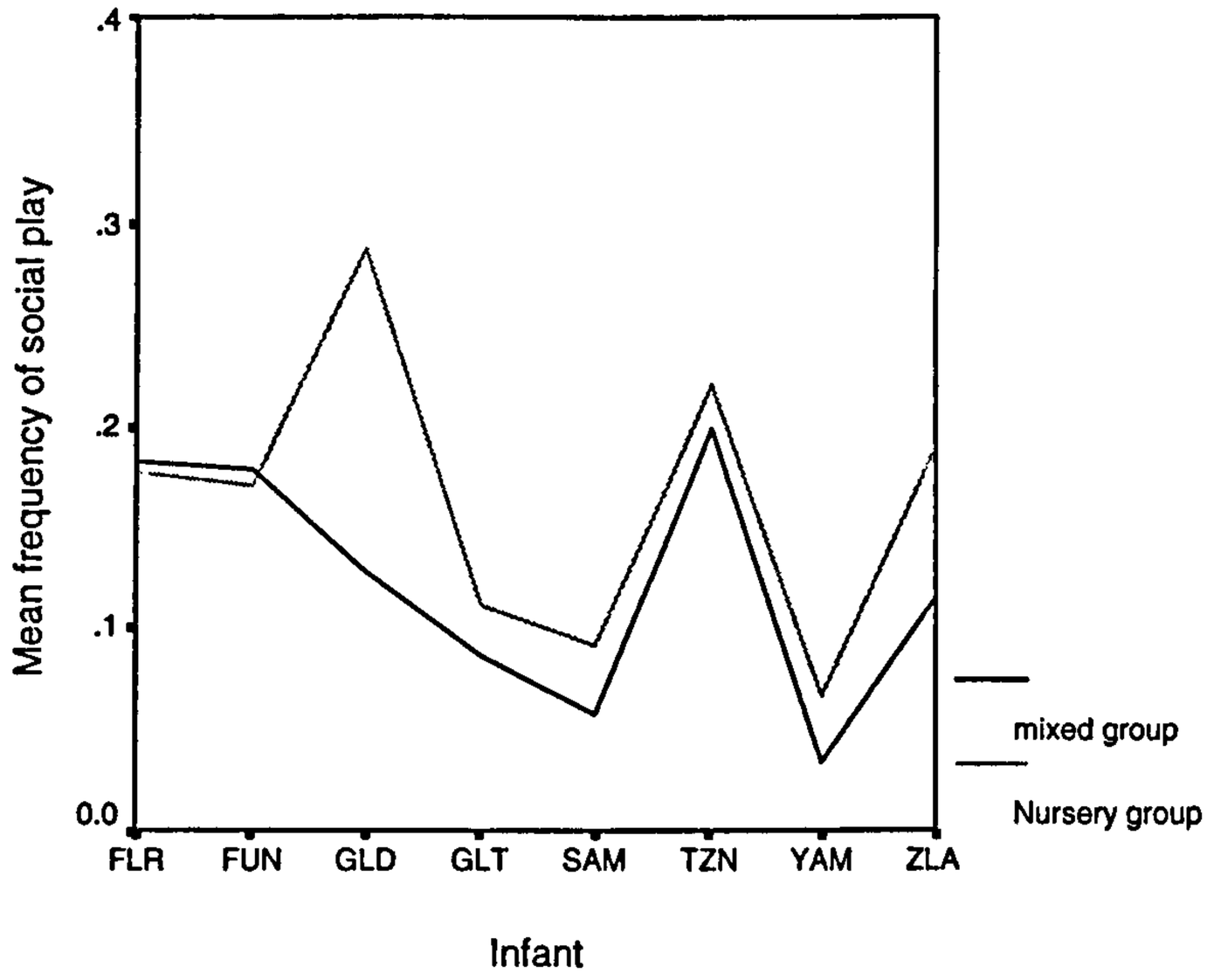


Figure 9: Line graph showing the overall frequencies of social play in nursery and mixed groups for eight infants.

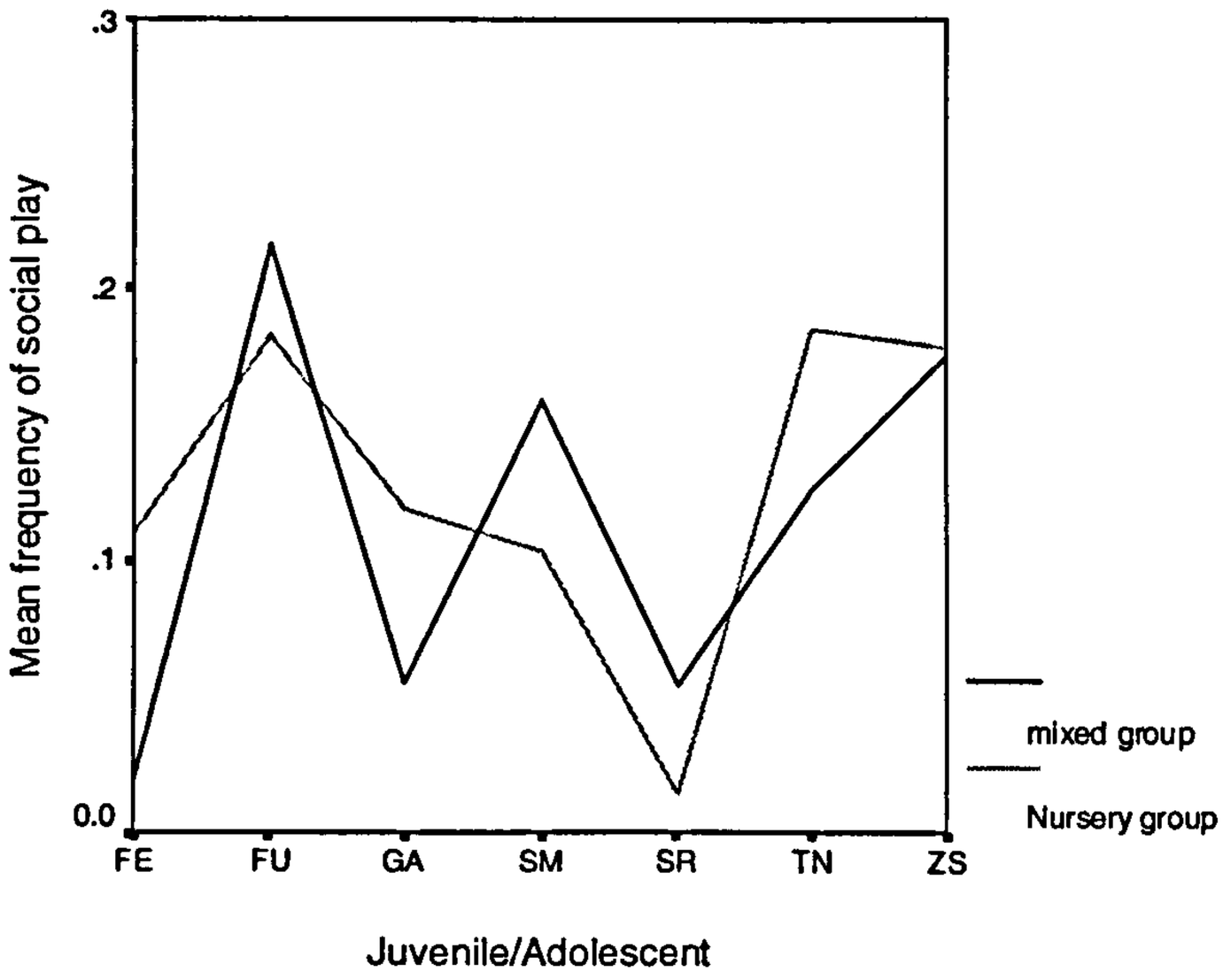


Figure 10: Line graph showing the overall social play frequencies in nursery and mixed groups for seven juveniles and adolescents.

Age wasn't correlated to average play session duration (Spearman's rho = -0.29; n = 17; p>0.05, 2-tailed). I investigated context as a determinant of play session duration. For this analysis I considered each session as independent and only used sessions where the context (resting, feeding and travel) were clear. This left a total of 640 sessions (feeding = 222, resting = 286, travel = 132). I performed a Kolmogorov-Smirnov test for

normality on the data but because the data was non-normal, performed non-parametric tests on the data. Figure 11 shows a box plot, showing the average duration focals spent in social play in the three different contexts. There was a significant difference in the social play duration between the three contexts (Kruskall-Wallis: chi-squared = 32.811; df = 2; $p<0.01$, 2-tailed). There was also a significant difference in social play duration between the two most similar groups, feeding and resting contexts (Mann-Whitney U = 27270.00; n1 = 222 feeding; n2 = 286 resting; $p < 0.01$, 2-tailed) indicating that the average duration of play in all three contexts were significantly different. Play lasted longer when the group was resting and least when the group was travelling.

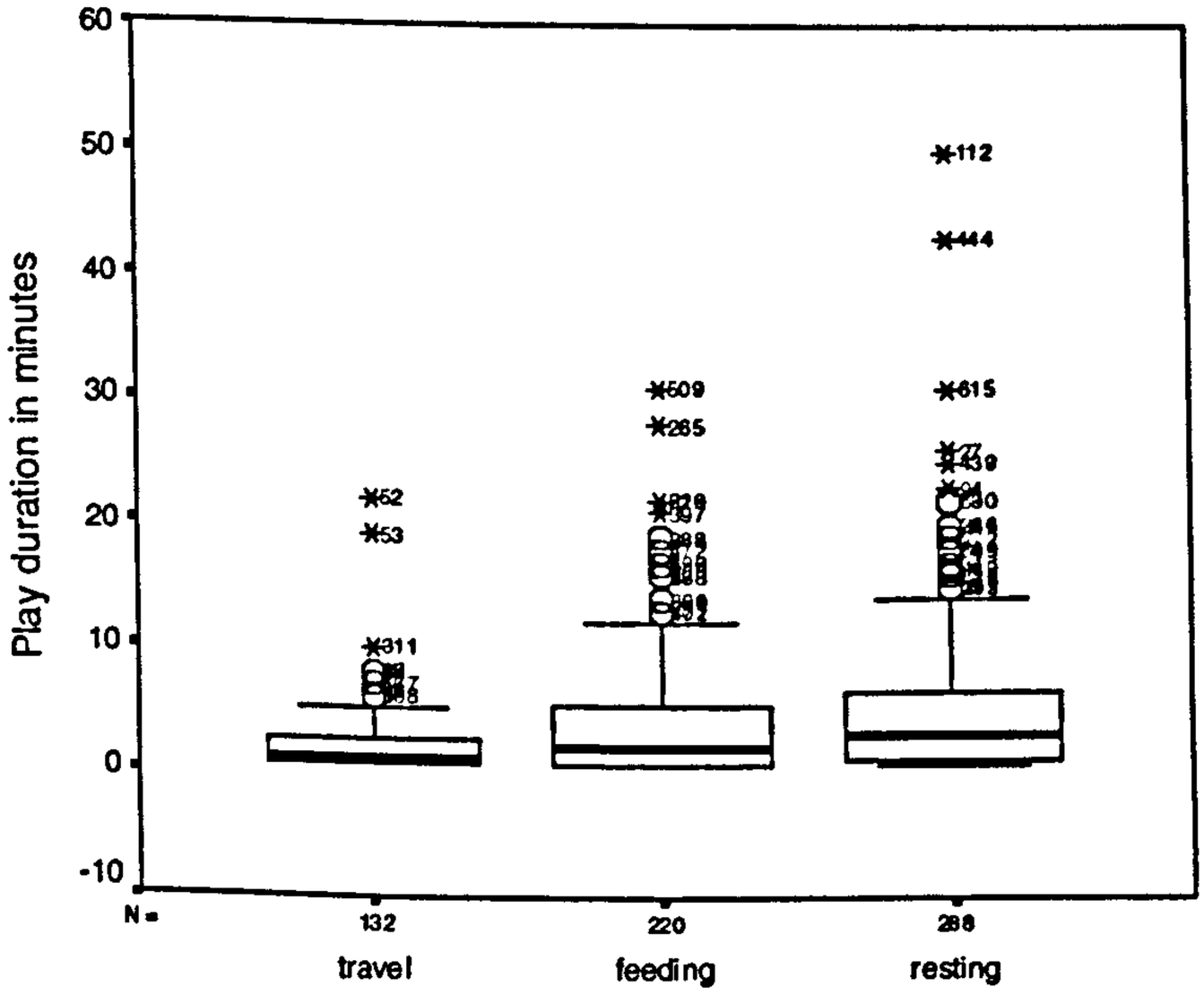


Figure 11: Box plot showing the average duration focals spent in social play in different contexts. Each plot shows the median, quartiles, extreme values and outliers in each category.

I investigated whether number of players in a session affected play duration by considering each session as independent and averaging duration across sessions with the same number of play partners (see figure 12). The mean play duration was significantly

correlated to the size of the playgroup (Spearman's rho = 0.45; n = 783 sessions; p < 0.01, 2-tailed), suggesting that playgroup size stimulates play duration.

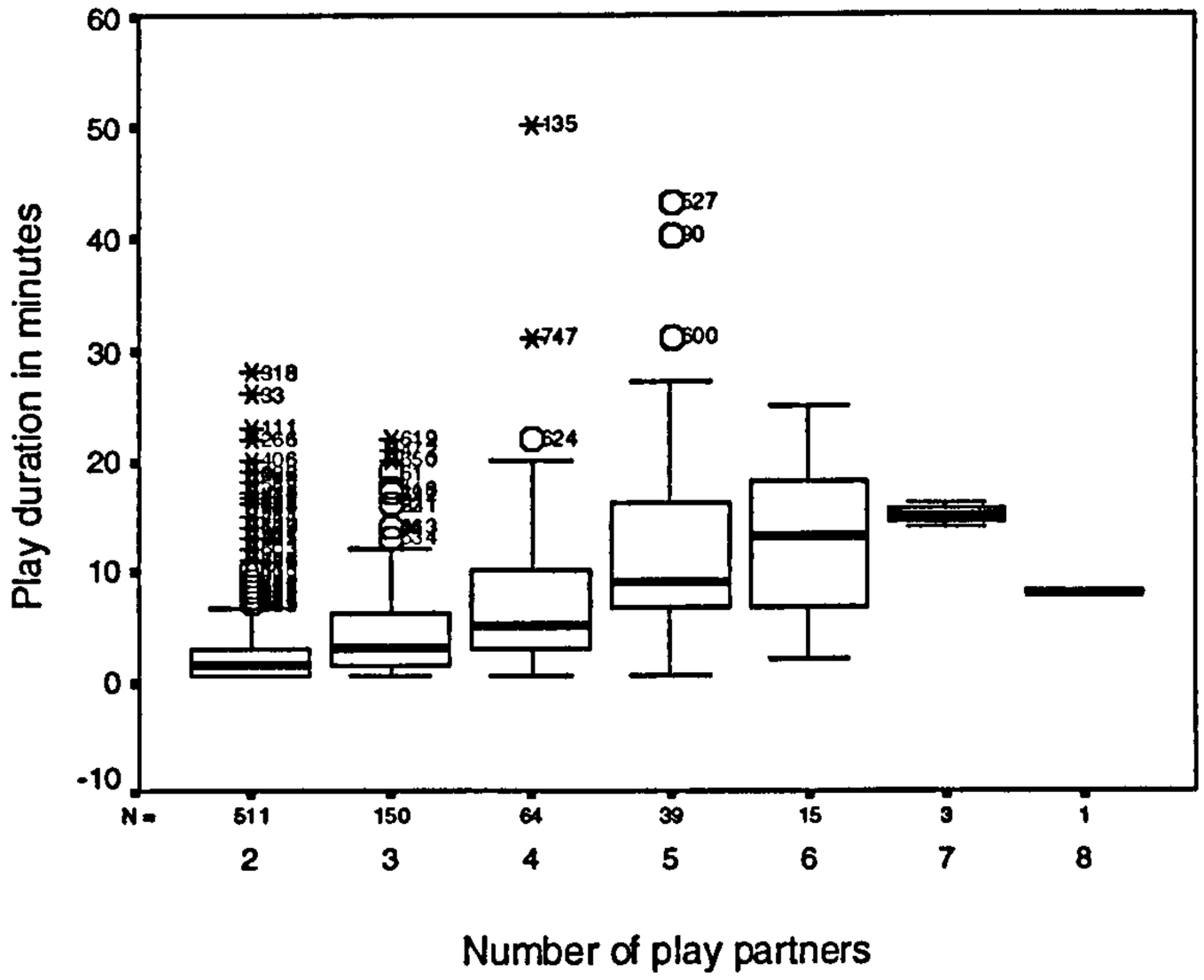


Figure 12: Box plot showing average play duration with focals in playgroups of different sizes. Each plot shows the median, quartiles, extreme values and outliers for each category.

I also investigated whether group composition had an effect on the duration with which the focals played. Again I considered play sessions as independent and averaged durations across the three group types: family, nursery and mixed. Groups composed of family plus one or two childless females were classed as family groups and sexual groups and gatherings were lumped as mixed. Although focal dependent offspring played for longer in nursery groups, the difference between the three groups was not significant (Kruskall-Wallis chi-squared = 4.349; n1 family = 203 sessions; n2 nursery = 249sessions; n3 mixed = 331 sessions; df = 2 p>0.05, 2-tailed). However, when I compared mean duration for juveniles/adolescents and independently travelling infants separately, there were strong trends for a difference between the average duration in the three group types (for juveniles/adolescents: Kruskall-Wallis chi-squared = 5.313; n1

family = 79 sessions; n2 nursery = 90 sessions; n3 mixed = 111 sessions; df = 2; p = 0.07, 2-tailed; and for independently travelling infants: Kruskall-Wallis chi-squared = 5.071; family = 86; nursery = 116; mixed = 136; df = 2; p = 0.079, 2-tailed).

3.3.3 Most Frequent Play Partners: Adults versus Dependent Offspring

In this part of the analysis, which seeks to identify most frequent play partners, social play frequencies were expressed as counts of the number of minutes in which the focal was observed to play with a specific individual, as a proportion of the total count of minutes that the focal played socially. Dependent offspring played on average at significantly greater frequencies with other dependent offspring, than with adults of the community (Wilcoxon signed ranks T+ = 31; n = 15; $p < 0.001$, 2-tailed). Dependent offspring therefore play with other dependent offspring over adults, either because close, physical and rigorous play with similar aged individuals involves less risk of injury; or because adults are generally less predisposed to play or inhibit their play responses in the presence of other dependent offspring, an effect found among captive squirrel monkeys *Saimiri sciureus* (Biben 1998).

3.3.4 Most Frequent Play Partners: Siblings

Dependent offspring played at significantly greater frequencies with siblings on average, (38% of social play time) than with other dependent offspring (10% of social play time) (Wilcoxon signed ranks T+ = 76; n = 12; $p<0.01$, 2-tailed). Furthermore the mean frequency of social play with siblings was significantly greater than the mean frequency of social play with other animals closest to the siblings' age and same sex (Wilcoxon

signed ranks T+ = 45; n = 10; p<0.01, 2-tailed). Offspring played more with their siblings on average than other animals of a similar age (Wilcoxon signed ranks T+ = 18; n = 13; p<0.001, 2-tailed), i.e. individuals who fell into the same age category as the sibling (infant, juvenile or adolescent). However dependent offspring didn't play with similar aged offspring more than other animals of a dissimilar age (Wilcoxon signed ranks T+ = 46; n = 11; p>0.05, 2-tailed). And contrary to the findings of other studies on a variety of species, chimpanzee dependent offspring also did not play more on average with similar aged or younger playmates than with older dependent offspring (Wilcoxon signed ranks T+ = 46; n = 12; p>0.05, 2-tailed) even when siblings were omitted from the analysis.

3.3.5 Most Frequent Play Partners: Maternally Related Kin

Offspring showed a tendency to play on average at a greater frequency with maternal kin (all adults and dependent offspring) than non-maternal kin (Wilcoxon signed ranks T+ = 31; n = 15; p = 0.1, 2-tailed). However, offspring of resident females who had never transferred permanently out or females who had emigrated into the community many years ago (in one case) did so significantly (Wilcoxon signed ranks T+ = 0; n = 11; p<0.01, 2-tailed). All of these females either had an adult mother/daughter and associating offspring, or brother in the community, with whom they shared a relatively close relationship.

For focal offspring, the proportion of total social playtime spent playing with different dependent offspring was calculated. Values ranged from a minimum of 0.2% to a maximum of 75%. The data points of dyads falling above the third quartile in the

distribution i.e. individuals that played with the focal for at least 20% of the focal's social playtime, were defined as most frequent play partners. All offspring had between one and four most frequent play partners (six focals had one most frequent play partner, six focals had two most frequent play partners, two focals had three most frequent play partners and one focal had four most frequent play partners). For all offspring whose mothers had no maternal relatives in the community (n = 4), most frequent play partners were unrelated, whether or not a sibling was present (in two out of four cases). For the eleven focal offspring whose mothers had maternal kin, seven played at the highest frequency with one of their siblings, while three played at the greatest frequency with either a nephew or uncle who was closer to them in age than a sibling. Only one focal played at the highest frequency with a non-relative, although she played at the second highest frequency with her infant sister. However, overall, ten out of the eleven focals whose mothers had maternal kin in the community had a sibling as a most frequent play partner. At the time of the study the sibling of the eleventh had, with maturity, dissociated himself with the family group, although in previous years he was undoubtedly a frequent play partner to his infant sister.

There was an almost significant negative correlation between the average frequency of play with maternal relatives and that of non-maternal relatives (Spearman's rho = -0.509; n = 15; p = 0.052, 2-tailed). Offspring who played less with maternal relatives played more with non-relatives on average, suggesting that in the absence of maternal relatives dependent offspring will seek out other members of the community to play with. Female dependent offspring played more on average with their maternal kin than male dependent

offspring but this was not significant (Mann-Whitney U = 21.00; n = 15; p>0.05, 2-tailed). However, there was an extremely strong trend for female dependent offspring to play on average at a greater frequency with their female maternal kin than male offspring (Mann-Whitney U = 7.00; males = 7; females = 6; p = 0.051, 2-tailed), while there was no significant difference between male and female dependent offspring in their average play frequencies with male kin (Mann-Whitney U = 10.00; males = 5; females = 4; p>0.05, 2-tailed). This is represented in figure 13. This sex difference may be extremely

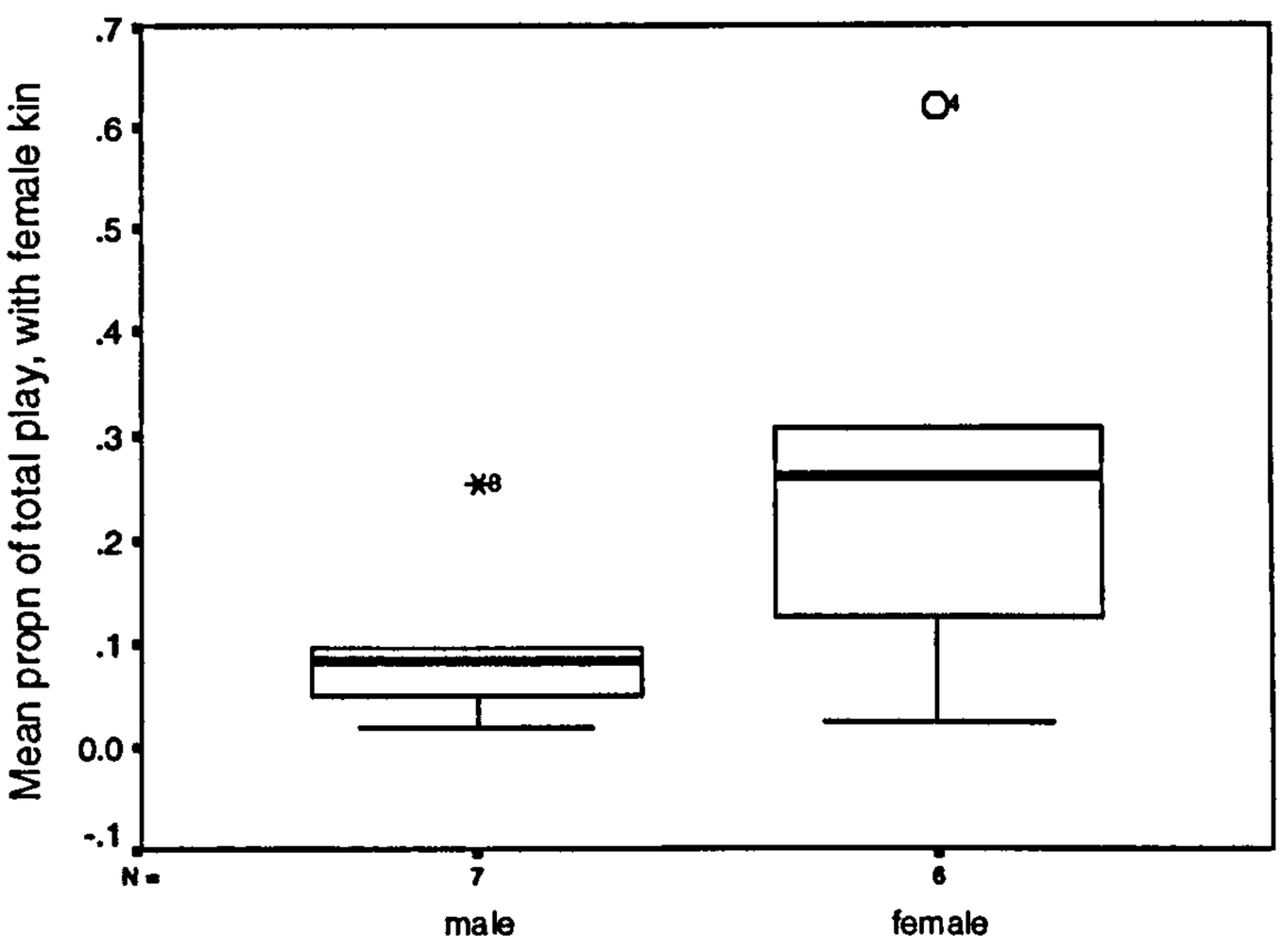


Figure 13: Box plot comparing the average frequencies of social play with female maternal kin (of any age) between male and female dependent offspring. Each plot shows the median, quartiles, extreme values and outliers for each category.

significant from a developmental perspective, since as adult, adult females at Gombe who do not disperse may rely on their female maternal kin for support (see chapter two), while support between males appears largely independent of relatedness. Expanding on this idea, and considering that adult males get support and form coalitions with adult males of a similar age, rather than their adult male kin, I tested to see whether male dependent

offspring play on average at a greater frequency with same sex companions of a similar age than female dependent offspring. I found no difference in the average frequencies with which male and female dependent offspring play with same sex companions of a similar age, although sample size was very small (Mann-Whitney U = 8.00; males = 4; females = 4; p>0.05, 2-tailed). Males did play on average at a greater frequency with male dependent offspring than with female dependent offspring, but again this difference didn't reach significance (Wilcoxon signed ranks T+ = 22; n = 7; p>0.05 2-tailed).

For each focal, the proportion of social play spent playing with different offspring was averaged across individuals who were related to the same degree, i.e. across siblings (r = 0.25-0.5), across aunts, uncles, nephews and nieces, (r = 0.125) and across individuals who were maternally unrelated (r = 0). This is shown in figure 14. As maternal relatedness between play partners increased so did average play frequency. There was a significant difference between the three groups in the average frequency of social play (Kruskall-Wallis chi-squared = 19.532; df = 2; p<0.001, 2-tailed). However there was no significant difference between the average social play frequencies of the two groups of kin, when they were either considered as two independent groups (Mann-Whitney U = 30.00; n1 = 12; n2 = 7; p>0.05, 2-tailed), or when the average proportions were compared across and between different focals (Wilcoxon signed ranks T + = 17; n = 6; p>0.05, 2-tailed). This suggests that while the average social play frequencies differed depending on whether the partners were maternally related or not, the degree to which individuals were related did not have an additional influence on social play frequencies.

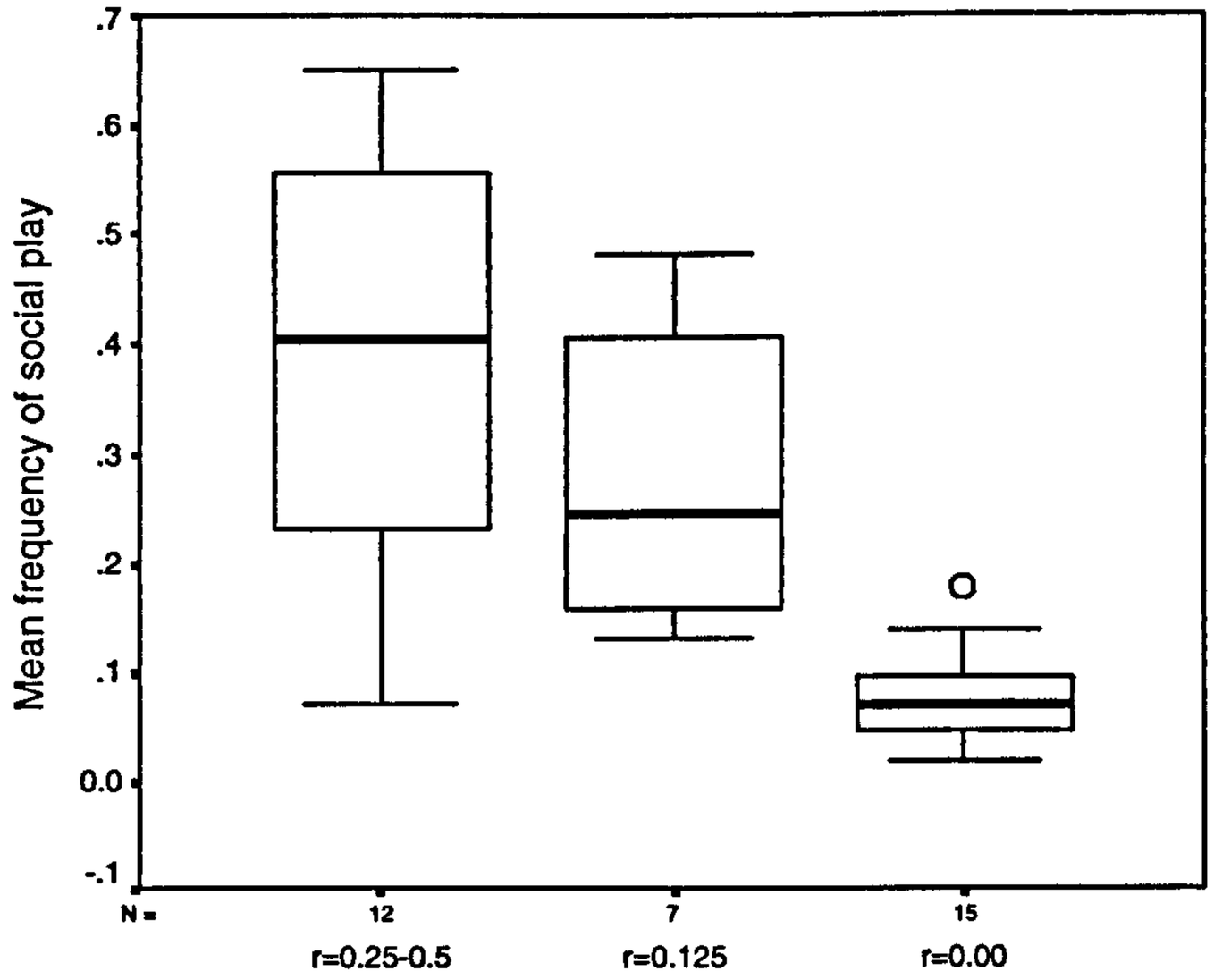


Figure 14: Box plot showing the mean play frequency against maternal relatedness. All siblings were assumed to be related by r = 0.25-0.5; for uncles, aunts, nieces and nephews r = 0.125; maternally non-related individuals r = 0.00. Each plot shows the median, quartiles and outliers for each category.

3.3.6 Social Determinants of the Mother: General Gregariousness

I investigated whether overall social play frequencies of dependent offspring were related to the general gregariousness of the mother. Following chapter two, I defined general gregariousness as the proportion of non-focal time mothers spent in groups composed of individuals outside her immediate family (her dependent offspring) and compared this to the overall play frequencies of her offspring. This relationship is represented in figure 15. There was an extremely strong trend that just missed significance (Spearman's rho = 0.503; n = 15; p = 0.056, 2-tailed). Mothers who spent more time in groups tended to have dependent offspring who played socially at higher frequencies.

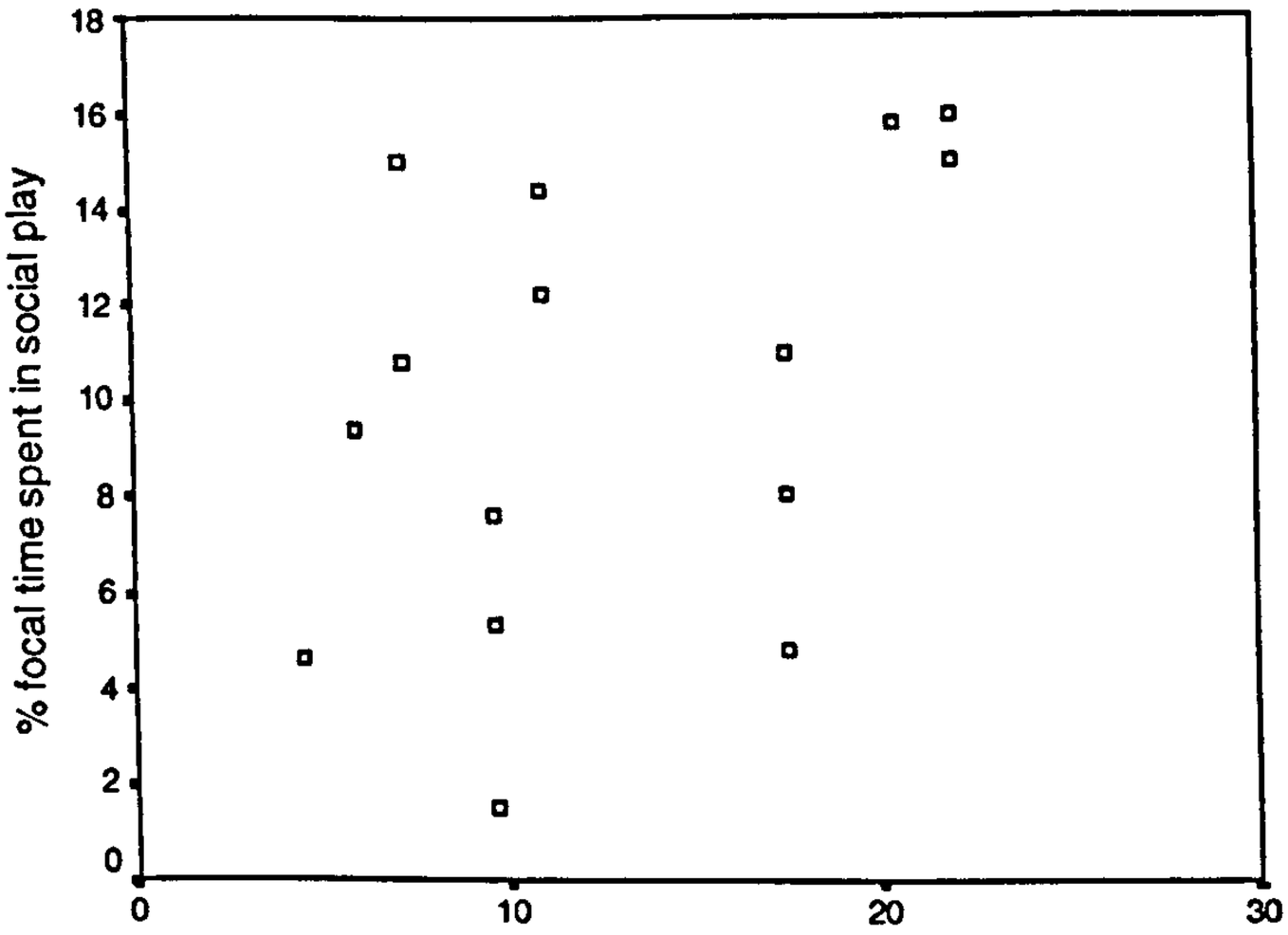


Figure 15: Scatter plot showing the relationship between the general gregariousness of the mother and the overall proportion of focal time her offspring spent in social play.

3.3.7 Social Determinants of the Mother: Dyadic Association Index

Figure 16 shows a scatter plot of the relationship between the social play frequencies between pairs of individuals and the dyadic association index (DAI) of the focal's mother with that of the play partner's mother (for details of the DAI see chapter 2). Each pair was considered as an independent point on the graph and sibling-sibling pairs were omitted. Since the play partners of some dyads (n = 35 dyads) were both subject to focal follows, for these dyads there were two social play frequency values (dependent upon who was the focal). I randomly assigned one of these values to the test group, reasoning that although there are randomisation issues (i.e. there are 35 to the power of two different possible combinations that could be assigned to the test group), had only one partner of each dyad been the subject of focal follows, this problem would not have arisen. The social play frequencies between different offspring outside the family group

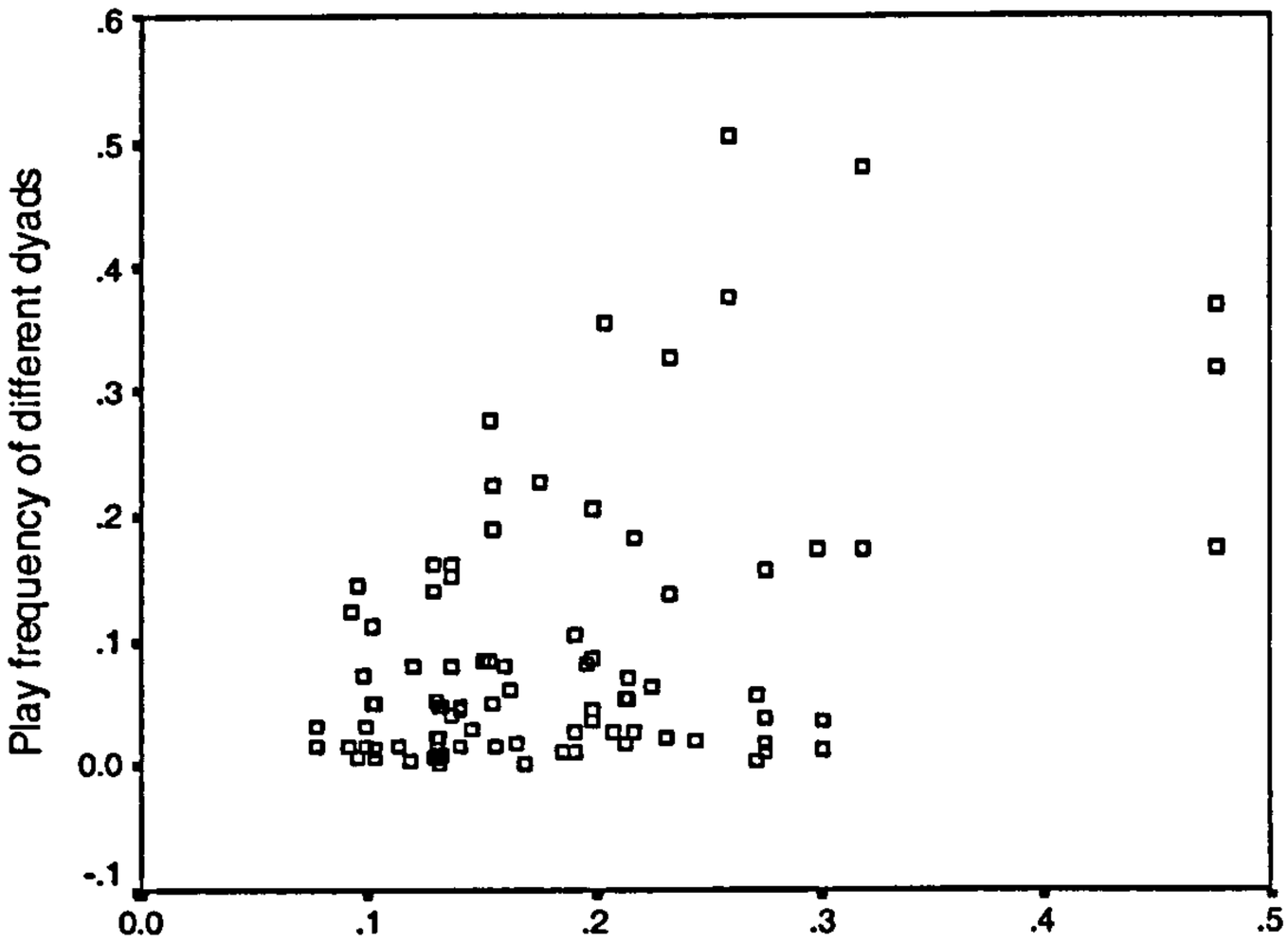


Figure 16: Scatter plot of the frequency of play between dyads of dependent offspring, against the DAI of the focal's mother with that of the focal's play partner's mother.

were significantly correlated to the level of association between their mothers (Spearman's rho = 0.322; n = 88 dyads; $p<0.01$, 2-tailed) and this still held when I tested the 53 dyads for which there was only one social play frequency value (Spearman's rho = 0.37; n = 53; $p<0.01$, 2-tailed). These results therefore suggest that the amount of play between specific individuals is highly dependent upon the level of association between their mothers. Offspring play at greater frequencies with those offspring whose mothers associate most together. When I averaged play frequencies and DAI's across independent offspring in the sample (n = 15), the average frequency of play with other individuals was significantly correlated to the average association of the mother with other mothers (Spearman's rho = 0.743; n = 15; $p<0.01$, 2-tailed), suggesting that mothers who associate more with other mother in general, produce offspring who play on average at a greater frequency. However when sibling pairs were omitted from the calculation of individual means, the trend did not reach significance (Spearman's rho = 0.411; n = 15; p

= 0.128, 2-tailed). This relationship was further strengthened by the finding that mothers who spent more of their grooming budget grooming adult females, or more of their grooming budget grooming both adult males and females, produced offspring who socially played more (Spearman's rho = 0.665; n = 15 offspring; $p<0.01$, 2-tailed; Spearman's rho=0.521; n = 15 offspring; $p<0.05$, 2-tailed; respectively).

3.3.8 Difference in the Relative Rank of the Mothers

Finally, I also investigated what effect, if any, the difference in relative rank of the mothers had on the frequencies of play between their offspring. Figure 17 shows a scatter plot of the relationship between the frequencies of play each focal had on average with the offspring of particular females, against the difference in relative rank of the offsprings' mother (see chapter 2 for details of relative rank). There was an extremely strong trend that just missed significance between these two measures (Spearman's rho = -0.214; n = 83 dyads; p = 0.052, 2-tailed). Offspring tended to play with other dependent offspring whose mothers were closer to their own mother in rank, on average, at higher frequencies than with offspring whose mothers were ranked further away from their own. This complements the above finding that females who associate most together have offspring who play most together, and the literature, which states that females closer in rank associate most together (Williams, Liu & Pusey 2002). However, when the average play frequencies of siblings were omitted the trend was no longer significant (Spearman's rho = 0.16; n = 71 dyads; $p>0.05$, 2-tailed).

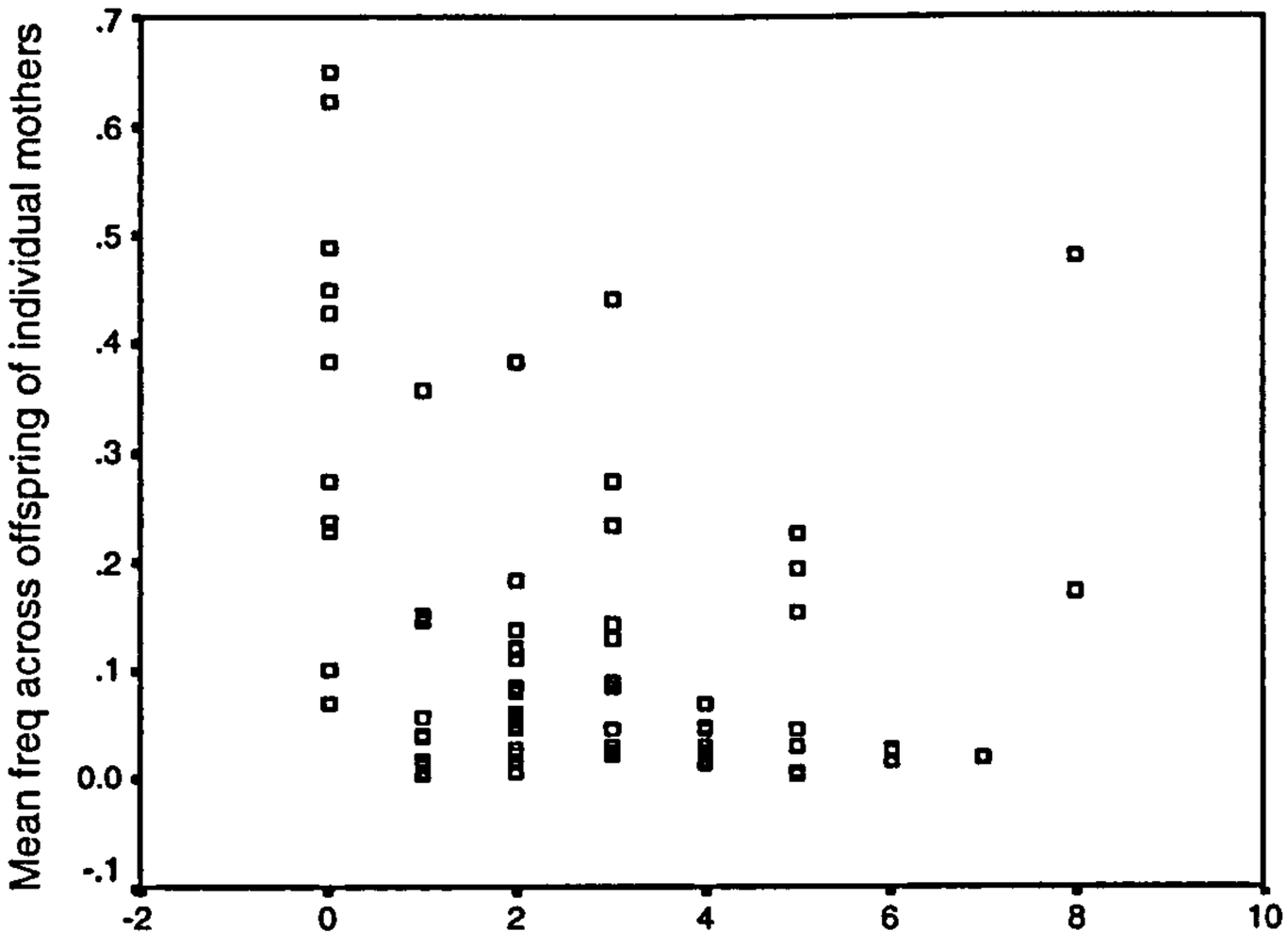


Figure 17: Scatter plot of the mean frequency of social play each focal had with the offspring of particular females, against the difference in relative rank of their mothers.

3.4 Discussion

3.4.1 Time and Energy Costs of Play Behaviour

The direct measurable costs of play fall into three major categories: an energy cost as a result of increased effort expended in performing play; a time cost, the result of using time playing that could otherwise be used on other beneficial activities such as feeding; and a cost to survivorship from injuries sustained in play or through increased risk of predation (Harcourt 1991). In terms of time spent in play there was a large variation among individual dependent offspring. Although not directly comparable due to differing methods of data collection and calculation, the range of values calculated (from 2-17% of total time) fall into the range recorded for other non-human primates (e.g. 3-14% for red colobus, *Colobus badius,* Clutton-Brock 1974; 20% for olive baboons, *Papio anubis*, Rose 1977 and Nash 1978; 3-5 % for chacma baboons, *Papio cynocephalus*, Cheney

1978; and 1-6 % for rhesus macaques, *Macaca mulatta*, Levy 1979; in Caro 1995). These values were also greater than those recorded for non-primate species (e.g. 3% in wild meerkats, 9%in laboratory reared domestic kitten, *Felis catus,* 1.5-6% in lions, *Panthera leo,* 2-3% in laboratory-reared rats, 3% in pronghorn fawns; in Caro 1995), suggesting that primates incur a higher time cost in playing. Although costs to survivorship were not assessed, predation risk for chimpanzees during play is probably very low. Distraction was an unlikely detrimental consequence of play, since dependent offspring's mothers, probably the main source of defence, were normally very close and relaxed during play. Although Goodall (1968, in Caro 1995) speculated that play could result in injury through falling, in six years of field research I never observed injuries occurring through play although there was one unexplainable disappearance of an infant whose mother, Sparrow, was observed without her infant, two days after being observed with her in the centre of the community range (*personal observation*).

Although no relationship between age and social play frequency was found, it is very probable that, like many other species, there is an age effect. The low values for early adolescents suggest that play may peak during the juvenile period and then decrease in frequency during early adolescence before immature chimpanzees disassociate themselves from the family group, as is found in baboons (Cheney 1978). Unfortunately sample size was too small to investigate this effect although previous work a marked decline at adolescence to exist (Pusey 1990).

3.4.2 Social Play, Diet Quality and Maternal Rank

Results suggest that there are significant differences in the social play frequencies of dependent offspring. Social play frequency was positively correlated to the diet quality (defined as proportion of fruit and nuts in the diet) of the mother and to the diet quality of independently travelling infants, supporting the notion in other primate species of a reduction in play frequency in response to a decline in resource availability (e.g. Lee 1984, 1986, in Barrett, Dunbar & Dunbar 1992; Biben 1998). A linear relationship existed between the social play frequency and diet quality of juveniles and adolescents, which didn't reach significance, probably because of low sample size. These results suggest that diet quality is a major determining factor for the occurrence of social play. Social play was negatively correlated with time spent feeding for juveniles and adolescents, suggesting that these individuals had both more time and energy available for social play. Furthermore, since high-ranking females and their adult daughters consume higher quality diets, probably through securing higher-quality feeding sites, their dependent offspring subsequently socially play at higher frequencies. This suggests that female rank not only determines the diet quality and reproductive success of individual females but also the diet quality and the energy available for dependent offspring's early social interactions. Alternatively, the fact that mothers with higher quality diets appear to be able to afford the costs of grouping and are subsequently more gregarious (see chapter two), suggests that mothers with higher quality diets bring their offspring into contact with the social environment more frequently, providing the right conditions for social play. This is supported by the findings discussed below. These results support other studies (see Harcourt 1991) showing that when food availability is

poor, play is suppressed; that is, play is extremely sensitive to prevailing conditions and is (according to some) a low-priority activity, which may be suppressed under natural conditions, implying that play is unlikely to be essential for normal development (Martin & Caro 1985) and provides only small benefits. However, if the costs of play are large, and they should be larger than more sedentary social behaviours, such as grooming, then there should be correspondingly large benefits. Because juveniles of most mammalian species are less constrained in terms of time and energy expenditure, devoting little of either into adult activities, in conditions of high food availability, they should be able to afford the energetic costs of play. However, energy is a major requirement of growth in juveniles and nutrient acquisition probably takes priority over social activities that don't provide immediate survival benefits, in environmentally stressed conditions. In some primate species, juveniles appear to adapt to conditions of low food availability, by decreasing their play activity and increasing grooming activity with their play partners (Lee 1983). This suggests that play's relative costs and benefits vary with the prevailing environmental conditions, more than other social activities and in times of food shortage, juveniles adapt by substituting play with less costly interactions, which may sufficiently provide a similar function, over the short-term, at least. This argument on the "lability" of play (Martin & Caro 1985) is somewhat circular, since play's persistent expression in times of food abundance could likewise be regarded as evidence for significant benefits.

To a point, these results support the Surplus Resource Theory of play (Burghardt 1988; ir Hall 1998) which explains the occurrence of play in terms of a response to nutritional conditions with consideration of the evolution of metabolic strategies providing surplus

energy resources available for play (Hall 1998). Burghardt (1988; in Hall 1998) predicted that species with a relatively large body size, prolonged parental care, which were not under nutritional stress and who were not constantly active and pushed to their physiological limits were more likely to play. This may explain the findings that play lasted longer when the group was resting, since offspring were thus able to use up their surplus energy, obtained while foraging, in "boredom" play.

Whatever might be the costs, benefits and functions of play, the offspring of high-ranking females and their adult daughters are socially interacting at higher rates than the offspring of other females. A similar effect was found for baboons by Cheney (1978), who speculated that as high-ranking females received more grooming and were groomed by more different individuals, their infants were brought into more regular contact with their peers. If play does teach and provide practise of social and physical skills that young animals will need for adult life, then the offspring of high-ranking females and their adult daughters may learn these skills quicker. While we talk about nutritional independence occurring on the completion of weaning, in a sense offspring are not nutritionally independent of their mothers until they disassociate from their mothers and family groups at maturity. Feeding competition among females has a potentially large impact on many aspects of their offspring's lives, including aspects of social development. For females who do not disperse, but set up core areas close to their mother's own, they in a sense inherit their mother's nutritional realm, with the potential to affect many aspects of their and their offspring's lives.

3.4.3 Social Play and Group Composition

Group composition had a large impact on the rate at which dependent offspring played. Offspring played at higher frequencies in groups where other dependent offspring were present than in groups where their dependent sibling(s) was the only potential playmate. Whether this was because offspring are inherently attracted to "novel" play partners, or simply a product of social facilitation, i.e. they were encouraged to play when observing other individuals do so remains unclear. Subsequently, dependent offspring played at higher rates in both mixed and nursery groups than family groups. Infants played at significantly higher rates in nursery groups than mixed groups, but juveniles and adolescents didn't, suggesting that nursery groups may provide an optimum environment for infant socialisation. This complements a recent finding at Gombe that females spend less time in mixed-sex parties and more time in female-only parties when they have an infant (Williams, Liu & Pusey 2002) due to costs associated with scramble competition. Interestingly, Bernstein & Draper (1963) in comparing play in different groups of rhesus macaques found that the presence of adults inhibited play. This study shows that dependent offspring played generally more in groups with adults, suggesting that if adults do inhibit play behaviour, other factors, such as the presence of other dependent offspring, overrides this effect. Biben (1998) showed that adult squirrel monkeys actually inhibited their own playful tendencies towards an infant, if other infants were present. Thus, it is also possible that dependent offspring have an inhibitory effect on adults in their presence.

Either novelty drives individuals to play, as has been found in some other species (e.g. Wood-Gush & Vestergaard 1991) or social facilitation (e.g. Negro *et al.* 1996) or more probably, a combination of both. Play duration increased with the number of playmates involved in the session and play occurred at higher frequencies and for longer durations in groups of dependent offspring who did not constantly associate together, i.e. in groups other than family groups where the only potential playmate was a sibling. Play rates among young chimpanzees match those of other non-human primate species that live in permanent social groups with a constant supply of social partners and overall level of play appears much higher in wild rather than captive groups of chimpanzees (Spijkerman 1986 in Brent *et al.*1997). This is surprising, since captive animals do not spend time searching for food and therefore appear to have more "spare time" for social interaction, while their wild juvenile counterparts spend a significant amount of time foraging alone in family groups. This supports the notion that novelty in a new set of social partners and the motivation to explore these "new" social relationships may drive dependent offspring to play. Often the first interactions between dependent offspring who have been separated both in time and space is to play and, as in an analogous social behaviour in adults, grooming, may serve to re-establish relationships between individuals, maintain familiarity and friendship (e.g. Pellis, Pellis & Mckenna 1993) and ultimately maintain group cohesion between individuals. In this sense play may serve an indispensable function for group living primates living in fission-fusion societies, driving individual chimpanzees to make extra use of opportunities to socially interact (Spijkerman 1986 in Brent *et al.* 1997).

3.4.4 Social Play and Maternal Sociability

Maternal associations determined both the rate of social play interaction between dependent offspring and also determined whom offspring associated with. Dependent offspring played at higher frequencies with those offspring whose mothers were closer in rank with the rank of their own mother, probably as a consequence of the findings by Williams, Liu & Pusey (2002) that females of similar rank associate most together. Supporting this, I found that social play frequencies between particular dependent offspring were positively correlated to the association between their mothers and overall social play rates were positively correlated to the proportion of the mother's grooming time spent grooming adult females. Furthermore, mothers who spent more time in groups and who associated more with other mothers on average, produced offspring who played at greater rates. This suggests that mothers determine the social milieu of their offspring and the offspring's social network mirrors that of its mother. Mothers who show strong preferences to socialise with other mothers provide social opportunities for their offspring, an effect found in baboons by both Altmann (2001) and Cheney (1978). The fact that this pattern continues from infancy, and through the juvenile and early adolescent period, suggests that as with other primate species (e.g. rhesus macaques, baboons) offspring function as members of their lineage from the beginning (Berman 1982). However, while these findings suggest ways in which dependent offspring develop social relationships, they fail to explain how relationships are sustained into adulthood. While there are similarities among offspring social play networks and adult female social networks, adult males and females who transfer, eventually develop very different networks to females. Interestingly, grooming reciprocity with mothers is

generally similar for male and female juvenile chimpanzees (Watts and Pusey 1993), unlike other species, such as baboons, where reciprocity is higher with daughters who are philopatric. This could reflect the fact that both males and females who transfer, mature to form different social networks precluding maternal support.

3.4.5 Social Play Networks: Residency and Degree of Relatedness

Offspring appeared to form stable social play networks, defined in terms of most frequent play partners. This selectivity was strongly related to kinship, a finding that is in contrast to some other primate species (e.g. baboons, Altmann 2001). All offspring had between one and four play partners who they played with at much higher rates than other offspring. Seven out of eleven dependent offspring, whose mothers had adult maternal kin in the community, played at the highest rates with their sibling, a finding similar to that found in marmosets (Stevenson & Poole 1982), and in juvenile baboons (Cheney 1978). The other three played most often with an uncle or a nephew who was closer in age than their sibling. Only one out of 11 dependent offspring, whose mothers had adult maternal kin in the community, played at a much higher frequency with a non-relative, and in this case the second most frequent playmate was her infant sibling. These results support findings by Brent *et al.* (1997) who found that more time was spent in social interaction with the sibling and Pusey (1978; in Pusey 1983) who found that dependent offspring interacted at higher rates with their infant sibling than other infants. For all offspring whose mothers had no adult maternal kin in the community, or in one case, shared no affiliative relationship with them, they played most often with a non-relative, whether or not they had a sibling. Furthermore, despite the fact that, overall, offspring didn't play on average more with maternal kin than non-maternal kin, for offspring of

females who had remained in the natal community and had not transferred, or had been resident for many years, and had consequently a network of maternal kin, these offspring played on average at higher rates with maternal kin. The average frequency of play increased with the degree of relatedness. Offspring played on average at higher frequencies with relatives than with non-relatives. However offspring who didn't have maternal relatives, particularly siblings, played more with non-relatives. This suggests that dependent offspring are active in initiating and participating in social interactions, and are not only recipients of interactions initiated by others (Brent *et al.* 1997) and therefore maintain an optimal level of interaction within the constraints of the mother's associations. Rather than place the sole responsibility for social interaction on the mother, it seems more reasonable that the mother-offspring relationship is a dynamic process involving input and feedback from each individual, which is modified by the social and physical environment (Brent *et al.*1997). Furthermore, the fact that offspring whose mothers had no maternal relatives in the community played at the highest frequencies with non-relatives, whether or not a sibling was present, may be an adaptive strategy or motivation to "widen" their individual social network.

Pusey (1990) found that juvenile offspring tended to play with offspring similar to them in age, when they were present. Pusey's measure was similar to one used by Berman (1982) on her study of rhesus macaques and took into account both the availability of play partners or the difference between play partners in their opportunity to interact and the duration of play sessions, calculated as the time spent playing with an individual as a proportion of the total time that individual was within proximity to the focal. In

retrospect, it is not too surprising that the measure utilised in this study reflected the extent to which mothers associated, since it did not take into account partner availability (although the fact that the associations of dependent offspring matching that of the mother, persisted over time, is less obvious). The measure utilised by Pusey (1990) and Berman (1982) would have complemented this measure nicely, by showing the extent to which offspring choose their play partners within the restrictions of their mother's associations. This was a point recognised by Berman (1982), who suggested that while the social network of a dependent offspring might mirror that of its mother, and stay intact over time, as the infant matures and grows more independent, he should take more of the responsibility of maintaining contact and proximity with other individuals. Over time, the quality of his relationships with particular individuals, with which his mother associates, might differ substantially from that of his mother. This certainly is a point worth noting for future studies of this kind.

There was no sex difference in the average frequency with which female and male offspring played with maternal kin. However, assuming that individuals of each sex had equal access to maternal kin, female offspring played on average at significantly higher frequencies with female kin than male kin, while no sex difference in play frequencies with male maternal kin was found. Therefore, the strong attraction between adult female kin demonstrated in chapter two and thought to be an adaptive strategy for support in agonistic interactions, appears to be present from an early age. Play by female dependent offspring may therefore serve to foster relationships between kin that have significant fitness consequences in adult life. In the Arnhem chimpanzee colony de Waal (1987)

found that female support largely depended upon existing social bonds. The fact that male dependent offspring did not play with male kin significantly more than female dependent offspring supports the notion that adult male coalitions are largely independent of previously existing social bonds (de Waal 1987) and maternal kinship. Mitani *et al.* (2002) found that males were more likely to support nonkin of similar age and status than kin, due to demographic constraints. However, analysis in this study did not find that male offspring played more with same sex and similar aged offspring. Although males played at greater frequency with other male dependent offspring, this did not reach significance. I suggest that male dependent offspring at Gombe are constrained by demographic factors such as a low number of like-aged, same sex playmates. Possibly in larger populations where there are greater numbers of male offspring of similar age, this effect would be more apparent, such as the Ngogo community, in Kibale Forest, Uganda, where there are 150 individuals. A study of Bushmen has shown that in small nomadic tribes, with only small numbers of children, children play in mixed age and sex groups, and only when tribes become larger do children segregate into particular age and sex play groups (Draper 1976 in Cheney 1978). It is therefore possible that play among individuals of different age and sex is more likely to occur in small groups. Alternatively, since adult males form coalitions which are largely opportunistic and less dependent upon past alliances, these effects could be absent because male bonding from an early age does not play a major role in future coalition formation. In this sense then play may be a forum in which immature individuals develop social behaviour and social relationships appropriate to adults of their sex (Pusey 1990).

3.4.6 Demographic Factors

Certainly demographic structure has been shown to affect the frequencies of particular behaviour patterns (Dunbar 1987) and the development of individual social relationships (Berman, Rasmussen & Suomi 1997). One of the most important variables governing the occurrence of play at any age is the availability of a playmate (Biben 1998) and the age/sex composition of the group at the time of an infant's birth. In infant sable antelope *Hippotragus niger,* partners of similar age are preferred (Thompson 1996) and births are both synchronous and seasonal, occurring annually. Unlike many other primate species, chimpanzee birth intervals are long and births are not seasonal or synchronous. As a result, peer groups of like-aged dependent offspring, present in many other primate species (e.g. baboons Cheney 1978, Altmann 2001), are not present in chimpanzee society. This may explain why kin preference may be a more important factor in the choice of play partner.

3.4.7 Intra-specific Differences between Populations

At Gombe, kin relationships between females appear extremely important and females order themselves into a consistent and stable hierarchy, possibly because competition for food may be higher than at other sites and in other populations. Along with differences in demography, this study begs the question of how differences in female social organisation, in different populations, affect the social development of dependent offspring. In populations where food availability is less varied in time and space, feeding competition is low, and rank effects are smaller, female association patterns may be more similar, and there may be less disparity between the social play rates of dependent

offspring. In populations where feeding competition is low, and support based on female kinship is less important, the choice of playmates may be less kin-dependent. Ultimately, how differences in the social experiences of young chimpanzees affects social performance as adults will shed light on play's adaptive significance and function.

3.4.8 Social Play Functions in the Role of Social Bonding

Whether or not social bonding is a primary function or an incidental benefit of play, as argued by some (e.g. Caro 1988), social play between immature chimpanzees has an important role in social bonding. By living in a group, chimpanzees may benefit from reduced predation and effective defence of resources and social bonding is the process by which individuals establish their identity and social relationships and maintain them through negotiation in a social setting. Social bonding is particularly important for adult males who must co-operate to defend a feeding territory (Williams *et al.* 2004) and important for adult females who are forced by male aggression to be members of one group exclusively (Williams *et al.* 2002). Females who are do not follow this pattern and don't appear to show strong allegiance to members of one particular community, are reproductively unsuccessful (Williams *et al.* 2002). Social bonding and group identity is, however, important to all individuals from all age groups due to the xenophobic nature of chimpanzees. All individuals, outnumbered by strangers from another community, suffer the risk of aggression and death and chimpanzees, particularly adult males, regularly patrol their community boundaries and execute raids into neighbouring territories. Infanticide also occurs within a community by both adult males and high-ranking females and in these cases, it is also possible that aggressors may perceive their victims as

outsiders. Therefore the threat of aggression, particularly that from adult males, may exert a selective force on all individuals to form intimate and supportive bonds within the group.

Although play fights superficially resemble true fights they do not include significant amounts of aversive stimuli. Players experience generous levels of positive reinforcement and this positive social conditioning is precisely the cause of social bonding and "friendship" (Baldwin, in Smith 1982). Play, I consider an analogous behaviour (in terms of its short-term, social, friendly, contact function) to grooming behaviour between adults. The link between play and grooming is illustrated by findings showing that the duration of grooming bouts among immature vervets with peers, tended to be longer during the dry season when there was little peer-peer play, and shorter when there was more play (Lee 1983); and among baboons, a shift in grooming partner preference from the mother to peers when play rates declined (Lee 1983). Unlike grooming however, play may not require large amounts of concentration or dextral competency that is probably beyond the cognitive capabilities of infant chimpanzees. In this light play can be seen as one strategy by which social relationships are established and maintained. The social bonding theory is strengthened by the finding that chimpanzees play significantly more when the environment permits social bonding to be particularly effective, i.e. in both nursery and mixed groups.

Many researchers of play behaviour have found that play is not essential for the development of adult behaviours of which play is thought to provide practice for (e.g.

Caro 1980, Martin & Caro 1985, Pellis & Pellis 1997), creating further debate on its possible function(s). While it may be an essential means by which young chimpanzees, at least, form relationships with other dependent offspring, social relationships can be formed and maintained by other means during other parts of the lifecycle of an individual. While newly immigrated females often can be observed playing with juveniles of their new community *(personal observation)*, they must resort to other strategies such as grooming and proximity maintenance, in dealing with adults. This is an important point to make, since many researchers have criticized the social bonding hypothesis by arguing that social play would not be expected to occur in the sex that disperses at maturity and cite the phenomenon that individuals who disperse at sexual maturity (often one of the two sexes) become adjusted to a new group with apparently little social play (e.g. Smith 1982). Such researchers are short-sighted in their arguments, ignoring the possibility that social bonding is an important pre-requisite of group living, for all age groups and ignoring the possibility that play is just one possible strategy used in social bonding. Social play is a potentially costly strategy for new immigrants associating themselves with strange adults in their new community. Inviting play with resident females, who may have extensive support networks, could be a costly way of establishing relationships, if they are generally hostile, as is the case at Gombe. The fact that new immigrants are often observed playing with older dependent offspring *(personal observation)*, suggests that social play can be used to establish new relationships in a new community. Its prevalence among the dependent offspring within a community suggests that it has a defined function in social bonding among community members, during development.

4 What is the Nature and Function of Social Play?

4.1 Introduction

4.1.1 The Nature and Function of Play: a Paradox

In this chapter I seek to closely investigate the nature and function of social play and in doing so provide suggestions on its adaptive significance in terms of immediate and delayed benefits. This is important because most functions of play predict benefits occurring later in ontogeny (Burghardt 1998), in part because play is a phenomenon of young developing animals and is generally believed to have an important role in the assembly of adult behaviour (Martin & Caro 1985); and in part because immediate benefits are hard to identify. While play is thought to be a rehearsal or specific developmental determinant (Bateson 1976 in Martin & Caro 1985) for adult behaviours, allowing individuals to practice motor skills related to intraspecific fighting and predatory skills, or for optimising skeleto-muscular development and increasing endurance (Fagen 1976 in Thompson 1998), there is very little quantitative evidence to support this and some evidence that runs contrary (e.g. domestic kitten, *Felis domesticus* Caro 1980; human children Humphreys & Smith 1984). As a result, certain explanations have been accepted more through a lack of alternatives than as a consequence of good scientific scrutiny. Because of the difficulties in identifying the adaptive significance of play, researchers have often concluded that it has a purposeless or neutral function. Motor patterns are defined as play because they appear to lack obvious consequences, at the same time biologists assume that animals only perform behaviour if the benefits outweigh the costs.

Undoubtedly a part of the problem in defining play, in terms of it's function, lies in the likelihood that play has evolved different functions for different species, different functions at different points in development and different functions for the same species living under different social and physical conditions (e.g. captive vs. wild). Because evidence supports the idea that play is a heterogeneous category, findings into the adaptive significance of play in chimpanzees may help other researchers studying this topic in other social primates. Social play defined by Fagen (1981) as involving two or more individuals that respond to each other's actions, was considered, since it was the most common form of play. Most social play among chimpanzees involves motor patterns involving R&T wrestle and chasing. While some researchers have chosen to study social, object and locomotor play separately, since they appear to develop at different times in ontogeny (Gomendio 1988), social play bouts in chimpanzees are often interspersed with elements of both object and locomotor play. For these reasons I assumed that any explanation for play could most satisfactorily be sought within the category of social play, since it appeared to act as an umbrella to other forms and categories and appeared the most important, occurring at the greatest frequency. While the study of social play may limit the extent to which inferences can be made on its function, some researchers agree that the chimpanzee may be an exceptional species, that social play may have been selected for the facilitation of social bonding and complex social skills (e.g. Smith 1982).

Social play in chimpanzees is primarily of the rough and tumble (R&T) sort, often interspersed with some chasing. For this reason, along with the fact that chimpanzees and

humans share comparatively recent evolutionary origins, comparison with studies on human children's R&T will be made where possible.

4.1.2 Hypotheses to Test

The hypotheses are:

1. Ha = Play is purposeful and goal directed

Ho = Play is purposeless

A related question to this is: is play competitive; do play partners compete for mutual goals or limited resources? If play is competitive does winning matter? In many species a dichotomous outcome of winner and loser is a feature of social play bouts (e.g. punares, Thompson 1998, see also Thompson 1998 for a review) as individuals attempt to gain some physical advantage over opponents.

2. Ha = Play has both immediate and cumulative benefits

Ho = Play has no benefits

This follows from the hypothesis above. If play partners compete for a mutual goal or a limiting resource, this suggests that there must be immediate benefits in winning, whether or not the benefits derive directly from the goal or resource, or why else should individuals play? If immediate benefits can be identified then delayed benefits may also be inferred. Whether or not these benefits are large, small, incidental or that for which the behaviour was originally selected for, is not a question of this study. Because most functional hypotheses have concentrated on benefits accruing later in life, identifying immediate benefits, despite the challenge, is highly important in itself.

3. Ha = Play functions to develop competitive and social skills and among the late juvenile period /early adolescence, to establish and maintain the dominance order.

Ho = Play doesn't function to develop and allow the practice of competitive skills.

Paquette (1994) concluded in a study on four captive adolescent chimpanzees that social play functioned in establishing and maintaining the dominance rank within dyads (Paquette 1994). However there are fundamental differences in the social structure of captive groups and wild chimpanzees that could have consequences for the functional significance of play. Related questions include: do dependent offspring order themselves into a dominance hierarchy in much the same way that human children in peer groups do and are status positions stable over time and across behavioural settings (Savin-Williams 1979)? What role does social play have in establishing dominance status and is this role equally important to each sex and across the age-span of the immature individual?

Information into the nature of play and its function was gathered from both videoed play bouts and focal follows on infant, juvenile and adolescent offspring. Because of the rapidity of play behaviours within a bout, analysis of video allowed for various characteristics of social play bouts to be identified, which could not have been recognized otherwise, and which proved insightful into the nature of play. Focal data was used to study most frequent play partners, age changes and sex differences in play behaviour and behaviours that co-occurred with play, primarily coercive ones, which play appeared to foster. This is a correlational study so while results lend support towards functional hypotheses they can neither refute or demonstrate that play is necessarily performing that

function (Martin & Caro 1985). However, other kinds of study, such as experimental ones, while providing more solid evidence, are impossible (and unethical) to implement in wild populations. While captive studies on chimpanzee play have been implemented (e.g. Paquette 1994), the differences in both the social and physical environment may well affect the nature of its function. Therefore, in order to gain insight into play's functional significance, captive studies can only complement studies on natural populations.

In this chapter I show that play is not purposeless, but, to the contrary, appears to be a competitive, affiliative interaction. Individual play partners appear to compete for mutual and highly desirable goals. I provide evidence to refute claims that play is used by individuals to assess both their and their partner's fighting ability, while providing further support for the "social cohesion" function and evidence for a social cognitive and social skills function. I show that aggression is an important consequence of play but, rather than being used to establish and maintain a dominance hierarchy, may be used to establish dominance status. While dependent offspring do not appear to order all their relationships into a dominance hierarchy, some dyads appear to have a fairly well defined dominance relationship. Finally, related to but independent of the "social cohesion" function, I propose a general function of social play that has ongoing benefits related to the ability of individuals to form socially competitive relationships, and I seek to redefine play based upon the findings of this study.

4.2 Methods

4.2.1 Play Video Analysis

Details of the study site, subjects and methods of focal data collection are described in chapters two and three. Social play was recorded onto mini DV tapes using a Sony digital camera (model DCR- TRV15E) from July 2002 and March 2003 during focal follows on dependent offspring and *ad libitum* sampling. Therefore, data from focal follows and that from videoed play bouts are not from entirely independent data sources. The video camera was carried during data collection periods and all well observed and unobstructed social play sessions involving dependent offspring were recorded where possible. There was a bias for social play to be recorded during feeding and resting periods and rarely while individuals were travelling, due to the brevity of play during the latter and the difficulty in recording and following simultaneously.

4.2.2 Analysis of Social Play Video: some Definitions

Sessions and bouts: Play was divided into sessions and bouts. Following Pusey (1990), I defined a session as a sequence of play uninterrupted by a break of two minutes or more. I further divided play sessions into units called bouts and defined a bout as a sequence of play uninterrupted by a break of five seconds or more. The definition follows that used by Stevenson & Poole (1982) but differs slightly to that used by some other primate researchers (e.g. Owens 1975a) but appeared appropriate with regards to the nature of wild chimpanzee play. A bout between a dyad was regarded as terminated when one of the players left the immediate vicinity to commence another activity and a new bout begun when one of these players started to play with another individual. If two players

stopped playing for five or more seconds while still in contact a new bout begun when play resumed. In a few cases A playing with B and A playing with C overlapped when C responded to A playing with B by joining and focusing his attention on A. If this overlap occurred for just a few seconds then the interaction was regarded as falling within two separate bouts since A terminated with B to play with C. If the interaction was prolonged then it was scored as a triadic bout.

Only play bouts that were dyadic in nature (involving two play partners interacting with each other simultaneously) and well recorded were used in the analysis. This was due to the problem of recording and defining social play involving multiple players. However, some triadic bouts, involving three play partners interacting with each other simultaneously, were included but treated separately, in order to draw further insight into the nature and function of social play. Hence, because some bouts of a session were omitted, videoed bouts were regarded as being part of the same session if they occurred within ten minutes of each other. Since many consecutive bouts were included and bouts from independent sessions were normally separated by a much greater time period, I was confident that I had labelled all sessions correctly.

Dyadic social playtime was taken from focal data and defined as any social play between just two individuals. Any minutes of social play involving more than two individuals was not scored as dyadic social play and thus this definition is a conservative one. It was possible, for example, that minutes of social play involving three individuals were either triadic play bouts or parts of two consecutive play bouts involving two dyads.

Since social play in chimpanzees can be made up of motor patterns that can be broadly categorised as R&T and chase, bouts were classified according to which motor patterns predominated. Videoed bouts were also analysed to try and identify the source of any competition. Since previous research had revealed that play partners sometimes compete for possession of an object or "toy", I wanted to find out just how common competition was, in order to estimate its importance as a fundamental characteristic of play. If resource acquisition was an important component of the play bout then the individual attaining the resource or achieving the objective of the "game" was identified as the winner, where possible.

Initiation: Initiation of a bout fell into three broad categories: a "play signal", such as the swishing of vegetation while looking at the play partner, "approach" with the intent to play, (individuals approached in a playful manner or approached while staring intently at the subsequent play partner) and approach to "contact", or if the partners were already within reach, "contact". Invariably approach followed play signal and contact followed approach although both play signal and approach were not necessary for an initiation (i.e the initiation of a bout could just be made up of contact). One or both of the play partners could have performed this series of behaviours, making up the interaction. Normally while one partner initiated "approach" the other initiated "contact". The individual performing the first initiation behaviour was recorded as the overall initiator. This is rather a loose term, so further to this, the individual initiating approach and the individual initiating contact were also recorded. While the individual initiating a play signal was also recorded, play signals were not always observed and were dropped in subsequent

analyses. If individual A approached individual B with an apparent intent to play and individual B didn't respond but individual C did (by making contact) then individual C was regarded as initiating contact, despite the fact that the approach initiation was not intended for him.

Termination: The terminator was considered that individual who voluntarily separated from his partner first. In the majority of bouts analysed, one of the partners moved away of his own accord. In dangle-play bouts however, often one individual was pushed and fell on vines or to the ground below. This was not scored as termination of the bout if the fallen individual resumed play by climbing back up to his play partner in less than five seconds. However, if this individual ran off or resumed another activity, he was scored as terminating the bout. If he took longer than five seconds to climb back up to his play partner, this was scored as a termination; his partner being scored as the terminator if he pushed him, or the fallen individual being scored as the terminator if he appeared to fall of his own free-will. Although slow-motion replay was an indispensable tool to use, termination and even some initiations proved particularly difficult to define (as they have in other studies e.g. Thompson 1996). In a few cases, an individual who had fallen ran off while looking back at his partner as if with the intent to initiate a chase, which his partner didn't respond to. In such cases the individual who initiated chase was scored as terminating the bout, because he was responsible of having terminated one "game" for another. In cases where a bout was terminated by aggression, the individual moving away, invariably the victim, was considered to terminate, although it could have been argued that the aggressor was responsible for terminating play by substituting play with

aggression. For this reason analyses on termination was done separately where the aggressor was considered the terminator and where the victim was considered the terminator. In a few cases both individuals appeared to terminate together, moving off simultaneously or in cases where the dyad remained in contact, stopping simultaneously. In such cases neither individual was recorded as terminating since neither party clearly had such a role.

Aggression: All aggressive incidents within play bouts were recorded. Coercive interactions were recorded as three types. *Rough* incidents were recorded when one individual gave a vocal protest such as cry or a squeal or a submissive facial expression such as a pout, in response to the actions of the other, or reached to hug his play partner for reassurance. After such interactions, play resumed immediately. *Aggressive* incidents were recorded when one of the play partners continued to cry, squeal or scream in response to continual rough subjection from the other. Such interactions could be followed by numerous behaviours, discussed in the results section, which invariably led to the end of the bout or the session. It appeared important to differentiate between these two types, since aggression in the former appeared unintentional, while in the latter it appeared intentional. Aggression in retaliation, such as hitting back at the aggressor while the aggressor was still being aggressive, was not considered in this study and occurred infrequently. In almost all cases the victim responded submissively and fights, in this context at least, were rare. A few interactions were labelled as *dominance* related incidents. In these cases the aggressor used subjectively aggressive behaviours, which didn't result in vocal protests by the target, but which invariably resulted in the two

separating. Such behaviours included very hard slaps or kicks and in one case an infant actually pilo-erected and charged at her playmate repeatedly, causing him to run to his mother. While the term "dominance" *may* be misleading (but see discussion section), the behaviours used were very similar to those used by adults during dominance conflicts (such as pilo-erection and charge).

4.2.3 Rates of Coercion from Focal Follows

Rates of coercion between different aggressor-victim dyads were calculated as the number of "coercive" minutes as a proportion of the total number of minutes the dyad was observed to play together (alone together and with other playmates). Rates were calculated separately where player A was the aggressor and player B the victim and where player B was the aggressor and player A the victim. Although there is arguably some pseudo replication involved, it was the relationship (i.e. aggressor-victim) rather than the dyad that was under investigation. Due to the problems in inferring whether "rough" incidents were intentionally aggressive in the same way that "aggressive" incidents were apparently intentional, and whether apparently dominance related behaviours were an intentional exertion of dominance, rates were calculated separately for all coercive interactions (aggressive, rough, dominance related: RAD), aggressive and rough interactions (RA) and aggressive interactions (A). Identification of the aggressor and victim meant that their degree of relatedness, the age difference between them, their age categories (e.g. infant, juvenile etc) and their sex could all be inferred or calculated. Well-matched dyads were defined as a pair of individuals who were both, infants, juveniles or adolescents. Ill matched dyads were defined as a pair of individuals who did

not fall into the same age category. For some parts of the analysis, infants were divided further into dependent infants who still rode on their mother's back during travel and independently travelling infants, since infancy, traditionally defined as being from 0-5 years (Goodall 1986), is a long period and older infants were markedly advanced in their development compared to younger ones.

4.2.4 Intra-observer Reliability and Analysis

To test for intra-observer reliability, 15% of the analysed play bouts were reanalysed, several months later. I calculated reliability scores as the percentage agreement between the two data sets, following similar methods used to test intra- and inter-observer reliability by Drea, Hawk and Glickman (1996). Intra-observer reliability scores exceeded 85% for the type of game played, what players were competing for and approach initiations and exceeded 75% for identification of the winner, terminator and who initiated contact.

Statistical analysis was performed using the SPSS statistical package. Due to low sample sizes non-parametric tests were used. Correlations were tested with Spearman's rho. The Mann-Whitney U test and the Wilcoxon paired ranks test were utilised in analyses involving two independent and dependent groups, respectively. All statistical tests were two tailed, with an exact significance threshold of 0.05. Significant tendencies were defined as tests that yielded a significance threshold of less than 0.1.

4.3 Results

4.3.1 The Nature of Play: Defining Play in terms of its Structure

350 videoed play bouts in 94 play sessions were analysed. 170 bouts were extracted from focal follows, while 180 bouts were taken *ad libitum*. 318 of these were dyadic bouts between two dependent offspring and 32 were triadic. Approximately 75% of the videoed dyadic play bouts could be classified according to what players competed for. 25% of these play bouts could not be clearly defined in this way either because competition seemed to occur at very low intensities or was apparently absent, or it remained unclear what partners were competing for. Dependent offspring competed for superior position, possession of an object such as a "toy" (often a piece of vegetation or a food item), or possession of an individual (in the case of triadic bouts). Because the majority of play bouts involved some form of competition, play can be viewed as goal-directed and purposeful.

Dangle-play was one "game" that used distinct motor patterns and where the object of the game appeared to be to attain a position above the opponent. This game in particular may be widespread among primates. I have observed it in the field among olive baboons *Papio anubis*, and on film footage of Japanese Snow Monkeys *Macaca fuscata*. Dangle-play occurred mainly arboreally. One or both of the players dangled from a branch and tried to ascend higher than their partner and/or pulled their partner down below them and/or pushed their partner so he fell to the ground, depending upon on the players' relative positions. Sometimes dangle-play occurred when one of the players sat on the ground beneath his dangling partner. Then the player on the ground attempted to pull his

partner to the ground in order to wrestle him. The goal of dangle-play was always very clear, with the lower positioned partner attempting to pull his partner below him while the upper player attempted to ascend out of reach. If there was a large discrepancy between the ages and sizes of the players then the nature of the game changed somewhat, proceeding more gently. Rather than push a small infant so he fell to the ground, his partner attempted to pull him down to his level. Such games were characteristically more one-sided and the roles of the partners non-interchangeable. Since a small infant was physically unable to pull or push his partner, he invariably was the one who climbed higher and out of reach, while his partner attempted to constrain him, pulling him to him. The winner was scored as the individual who was able to maintain the upper position or who pushed his partner below him the most often. In cases involving ill matched play partners, the larger was scored as winning if he was able to constrain the infant for the majority of the play bout, which in almost all cases he was able to do. In cases where one individual was dropped to the vines or ground below, thus terminating the play bout, the individual remaining in the branches above, was scored as the winner.

Another kind of "game" for superior position was wrestling. The goal here seemed to be to pin the partner to the ground by maintaining a position over the top of him. Wrestling was invariably fragmented and interspersed with chasing and lying side by side on the ground, play biting and tickling. If there was a large age or size discrepancy, the nature of the game changed also, with the larger individual appearing to constrain the younger one while possibly self-handicapping himself. In this sense, then, not as many wrestling bouts appeared truly competitive or goal-directed as dangle-play bouts. Although the winner

was scored as the player who was able to pin his partner down the most often or successfully, sometimes a winner could not be deciphered due to the fragmented nature of the game. Often wrestling and dangle-play were combined within bouts.

The second goal-directed "game" involved competing for possession of an object. Such objects could be a "toy" such as a seedpod, a leafy branch, a monkey's tail or a rag deposited by a human, which was wielded in a playful manner in front of the opponent. In some cases the object was a food item that one player was feeding on. Objects were very variable, however, and could be anything attractive in the physical or social environment. In a few instances, the object was a rock, which players competed to hug or sit on, blurring the distinction between competition for an object and competition for superior position. In one case, a female player initiated play with a juvenile male, by playfully competing for possession of a female's anogenital swelling that the male was trying to copulate with. This could either be considered as competition for the possession of an object or interference (see below). The motor patterns used were a combination of those mentioned above: chases, dangling in a tree or wrestling on the ground for possession of the object, interspersed by playful poking or hitting. Sometimes the object was discarded as the bout switched to competition for superior position. The winner was scored as the individual who was able to maintain possession of the object most often.

The third type of goal-directed "game" involved playing for possession of another individual that occurred in bouts of three individuals, predominantly where one of these individuals was a small infant. The two larger individuals often competed directly for

possession of the small infant by grabbing a limb and pulling in a tug'o war fashion, or indirectly by trying to instigate the desired player in two separate games simultaneously. A similar game has been described in baboons; infant carrying occasionally developed into a game in which two or three juveniles, nearly always females, competed for possession of an infant (Owen 1975a).

In a few bouts (n = 9), individuals appeared to interfere with an older individual who was trying to resume a different activity such as feeding or grooming and in one case copulation. The older individual was able to resume this activity while playing intermittently, or playing first then resuming the activity. In these bouts the younger offspring appeared to try and disrupt another's behaviour and although the other played with him, play did not appear mutually desired.

In conclusion, then, chimpanzee social play can be classified according to the mutual goal of the players, who compete for: a superior position, possession of a prized object, or possession of another individual. Bouts can be made up of combinations of the above and use a variety of motor patterns. For example, a bout could be initiated with a "toy," which could be discarded to develop into dangle for superior possession, to wrestle for superior position, to wrestling for possession of a toy again.

Analysis of the play video suggested that the degree of competitiveness might vary depending on the ages of the play partners, an aspect of play that deserves further study. It was my impression that in dyadic bouts involving a young infant (less than 2 years

old), the older play partner appeared to be restraining and manipulating the infant's behaviour, rather than competing directly with him. Over 85% of the dyadic bouts that could not be identified as clearly competitive (77 bouts in total) involved play with an infant under 5 years, and 61% of these bouts involved play between an infant and a juvenile or adolescent. There was therefore a positive association with which infants were involved in apparently non-competitive bouts (chi-squared = 39.286; df = 1; p <0.0001, 2-tailed).

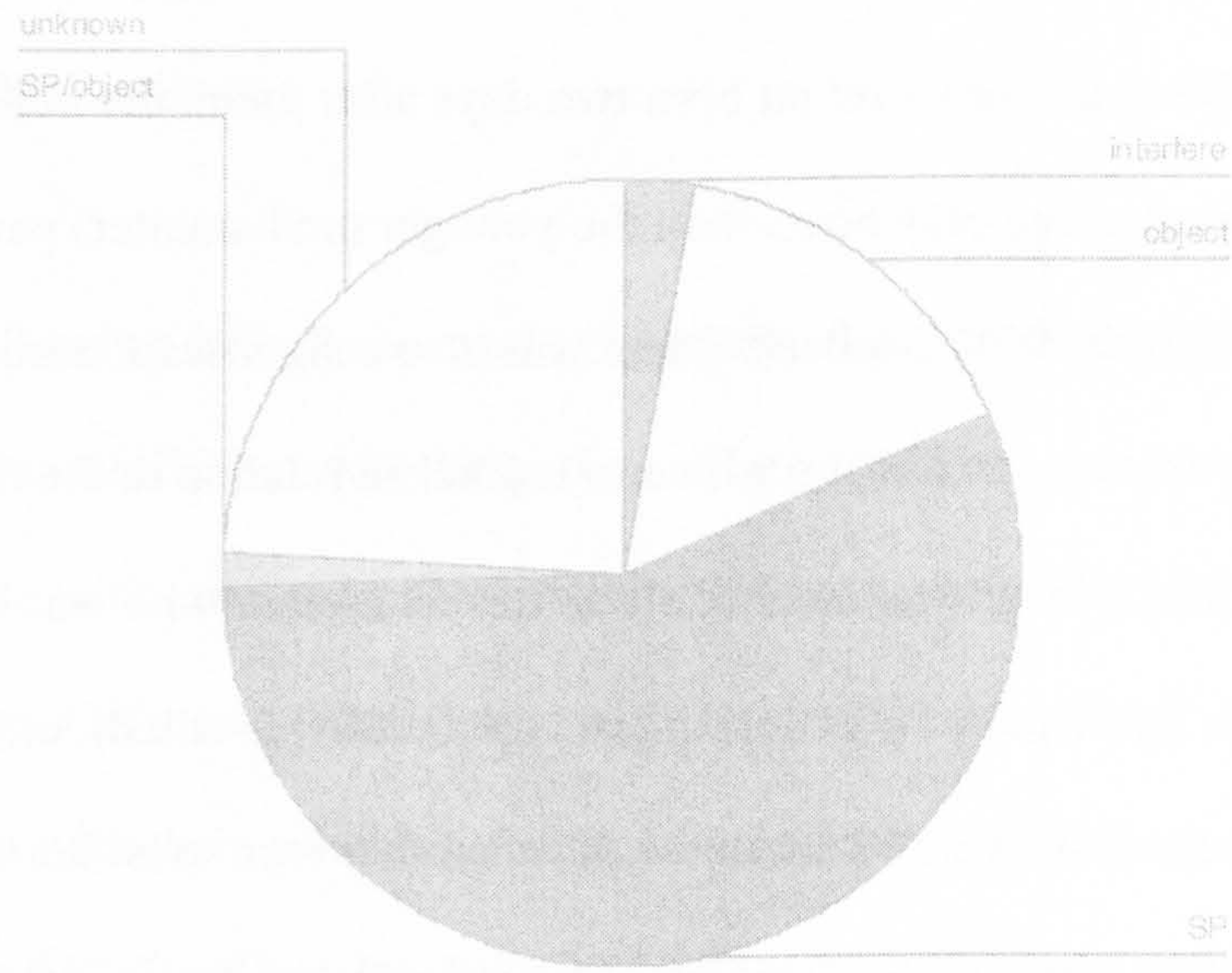
Very occasionally during play, an older individual cried when a young infant moved off; this behaviour is difficult to interpret since it appeared to occur in the absence of rough or aggressive behaviours. In one observed case an adolescent female started crying when a year old infant moved away from her laughing, possibly because her inability to control his behaviour or the direction of play caused her stress.

The majority of dyadic bouts involved competition for the superior position. A relatively high percentage of triadic play bouts (37.5%) involved competing for another chimpanzee, as compared to none of the dyadic bouts. These percentages are not comparable since only a selection of videoed triadic bouts were analysed, whereas all well observed dyadic bouts outside the travel context, when play was often brief and not well observed, were included. However, this observation points to the fact that that over which play partners compete may change with increasing number of play partners involved, and competing for another individual is characteristic of triadic play and possibly play involving more partners.

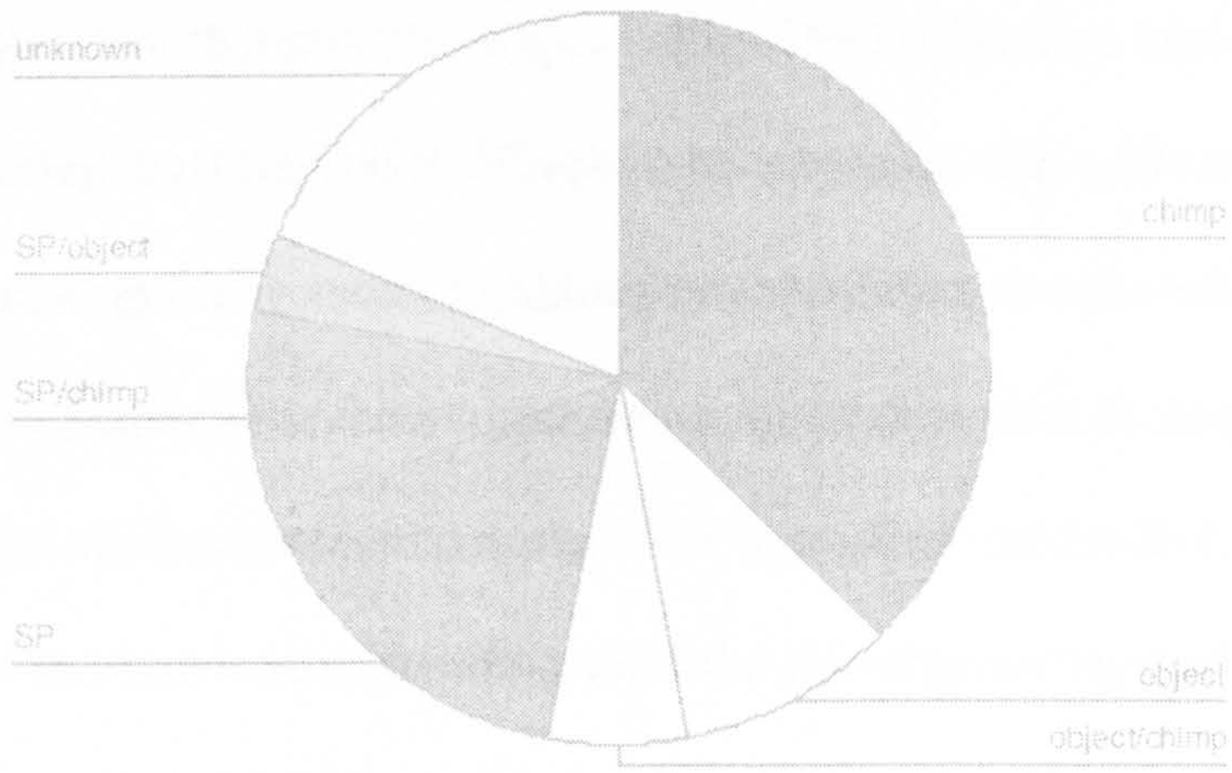
Figure 1 shows the proportions of bouts for both dyadic and triadic play that were classified according to what the players competed for. From 2493 minutes of social dyadic play involving dependent offspring, there was 91 minutes involving rough or aggressive interactions, at a rate of 0.0365 interactions per minute. Out of 625 focal minutes of social play involving dependent offspring and three individuals, there were 39 minutes involving rough or aggressive interactions, at a rate of 0.0624 interactions per minute. Coercion therefore occurred approximately twice as frequently during minutes of social play involving three players than those involving two. These are not necessarily triadic bouts involving three players simultaneously and therefore inconclusively prove that competition for an individual may explain heightened levels of aggression. However, out of 32 videoed play bouts between triads, 12 bouts in 11 play sessions included rough or aggressive incidents, 8 bouts or 67 % of which were competition over the possession of one of the players.

4.3.2 "Rules of the Game": Characteristics of Dyadic Play Bouts

The following section analyses various characteristics of dyadic play bouts. If bouts are truly competitive then the loser should be more motivated to terminate the bout, and this is what was found. In over 65% of the play bouts analysed, the identified loser terminated the play bout, and termination was associated with losing (chi-squared = 18.225; df = 1; $p<0.0001$, 2-tailed). Even in play bouts ending with aggression where the aggressor was arguably the terminator of the play sequence, this association still held (chi-squared = 5.70157; df = 1; $p<0.02$, 2-tailed). There was also a significant association between the



Dyadic



Triadic

Figure 1: Proportions of dyadic and triadic bouts videoed and analysed, classified according to what the players involved in the bout were competing over. The proportions between dyadic and triadic are not directly comparable since only a sample of triadic bouts were analysed. However the pie charts show that the number of players present may affect the nature of competition. SP = bouts where individuals were competing for superior position.

age (and presumably the size) of the play partners and the winner. Omitting play bouts between twins and both twins and another infant born two days after them, the older (and larger) player won significantly more play bouts than the younger (and smaller) partner (chi-squared = 64.47; df = 1; $p<0.0001$, 2-tailed). There was also a significant association between the winner and the relative rank of the winner's mother in relation to the relative rank of the loser's mother. The winner was more likely to have a mother who was higher in rank to the loser's mother (chi-squared = 20.21; df = 1; $p < 0.0001$, 2-tailed), omitting dyadic bouts between siblings. However, although the older partner won most bouts and the loser terminated more often, the younger member of each dyad was not found to terminate more often (chi-squared = 1.729; df = 1; $p < 0.2$ 2-tailed). There was, however, a significant association between the age/size and maternal relative rank of the dyad members and initiation. Overall there was a tendency for the younger member of the dyad to initiate more often (chi-squared = 2.7479; df = 1; $p < 0.1$, 2-tailed) and to initiate approach significantly more often (chi-squared = 11.376; df = 1; $p < 0.001$, 2-tailed). There was also a tendency for offspring with a lower-ranking mother, in relation to that of the play partner in the dyad, to initiate more approach initiations (chi-squared = 3.085; df = 1; n = 117 bouts; $p <0.1$, 2-tailed). In light of these results, there was a tendency for the loser to initiate significantly more approach initiations (chi-squared = 3.27; df = 1; n = 135 bouts; $p <0.1$, 2-tailed) and the winner to receive more approach initiations (chi-squared = 2.94; df = 1; n = 136 bouts; $p <0.1$; 2-tailed). The play partner who received more approach initiations was not only the older individual but also had a higher ranking mother relative to that of his play partner (chi-squared = 6.923; df = 1; $p < 0.01$, 2-tailed)

and in response, initiated the most contact initiations (chi-squared = 6.32; df = 1; p < 0.02, 2-tailed).

Following from these results, I hypothesised that if the aim of play is to compete successfully for something, then offspring should spend more of their dyadic social play time with younger individuals and offspring whose mothers are lower ranking than their own. Offspring didn't spend a greater proportion of their dyadic social playtime (omitting that with their siblings) with younger offspring (Wilcoxon signed ranks T+ = 76; n = 14; p > 0.05, 2-tailed. Juveniles and adolescents didn't spend a significant amount of this time with younger offspring (Wilcoxon signed ranks T+ = 18; n = 6; p > 0.05, 2-tailed) but there was a strong trend for independently travelling offspring to do so (Wilcoxon signed ranks T+ = 15; n = 5; p = 0.063, 2-tailed). Offspring also did not spend a greater proportion of their dyadic social play time with offspring whose mothers were lower ranking than their own (Wilcoxon signed ranks T+ = 53, p> 0.05, 2-tailed). Even when analysing data separately for adolescents/juveniles and independently travelling infants, there was no significant association (Wilcoxon signed ranks T+ = 13; n = 6; p> 0.05, 2-tailed; Wilcoxon signed ranks T+ = 9; n = 5; p> 0.05, 2-tailed; for juveniles/adolescents and independently travelling infants respectively). Figure 2 shows a scatter plot of the proportion of dyadic social playtime spent with offspring whose mothers were lower ranking than their own (omitting siblings). There was a significant negative correlation between the proportion of this time spent with offspring whose mothers were lower in rank to their own and the relative rank of the mother (Spearman's rho = -0.658; n = 14; p < 0.05, 2-tailed). In other words, as maternal rank increased or decreased, offspring were

increasingly constrained by the number of potential play partners whose mothers were higher or lower ranking, respective to their own. If the association between winning and maternal rank is a true effect it suggests that this factor is not within the control of offspring, since they are constrained by their mother's rank.

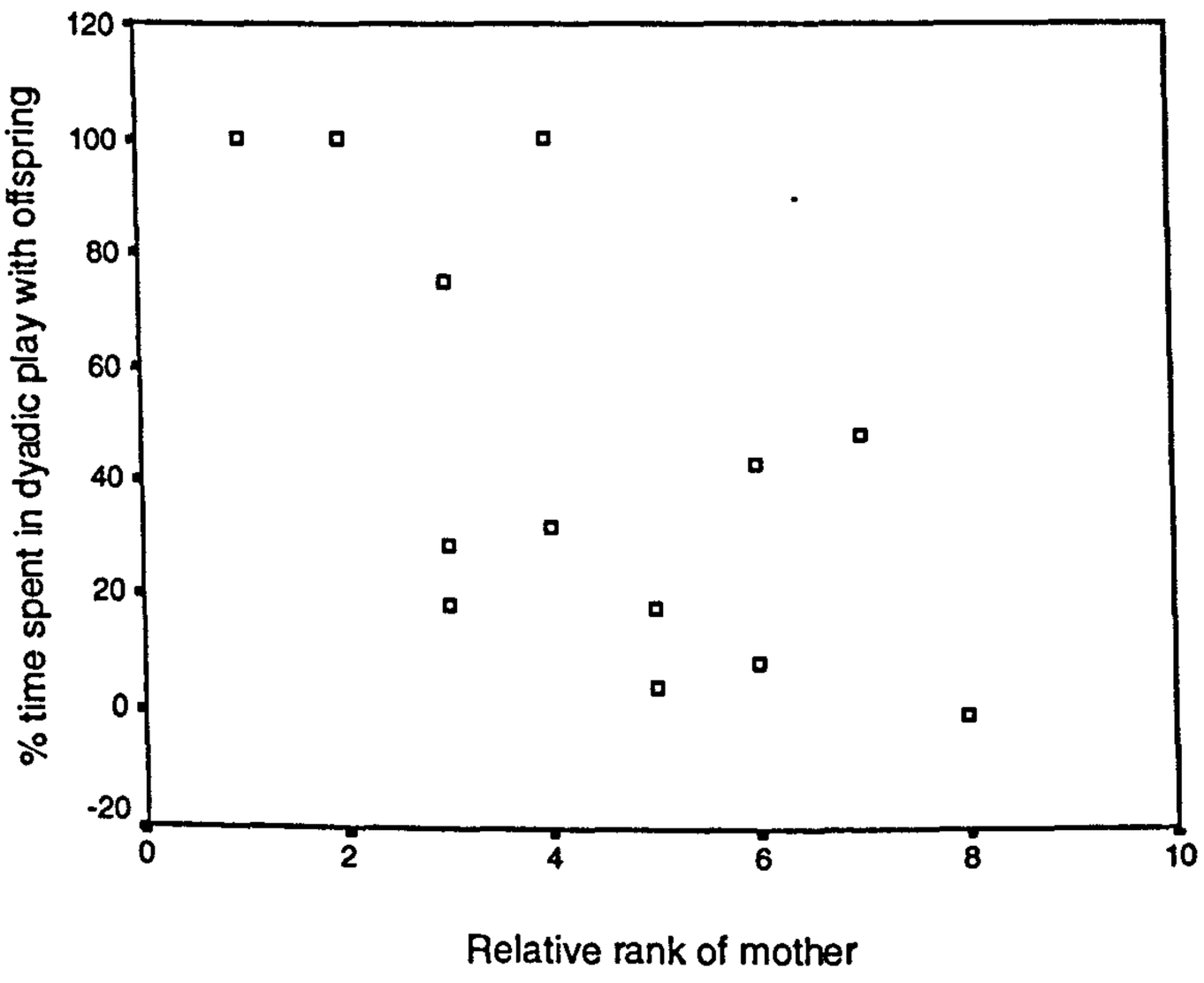


Figure2: Scatter plot of the relative rank of the mother against the proportion of social dyadic play time with offspring whose mothers were lower ranking than their own. Here the highest-ranking female has a relative rank of 1 and the lowest-ranking female a relative rank of 8.

Figure 3 shows a scatter plot and a linear relationship between the relative rank of the mother and the proportion of social dyadic play spent with younger offspring. Offspring of high-ranking females spend a greater proportion of their social dyadic play with younger individuals than offspring of lower-ranking females (Spearman's rho = -0.541; n = 14; $p < 0.05$, 2-tailed), suggesting that offspring of higher-ranking females should win more of their play bouts. This could therefore explain why high maternal rank was associated with winning. Why offspring of higher-ranking females should bias their play

towards younger individuals, remains unclear but these offspring appear more competitive, using strategies related to partner choice, in order to win.

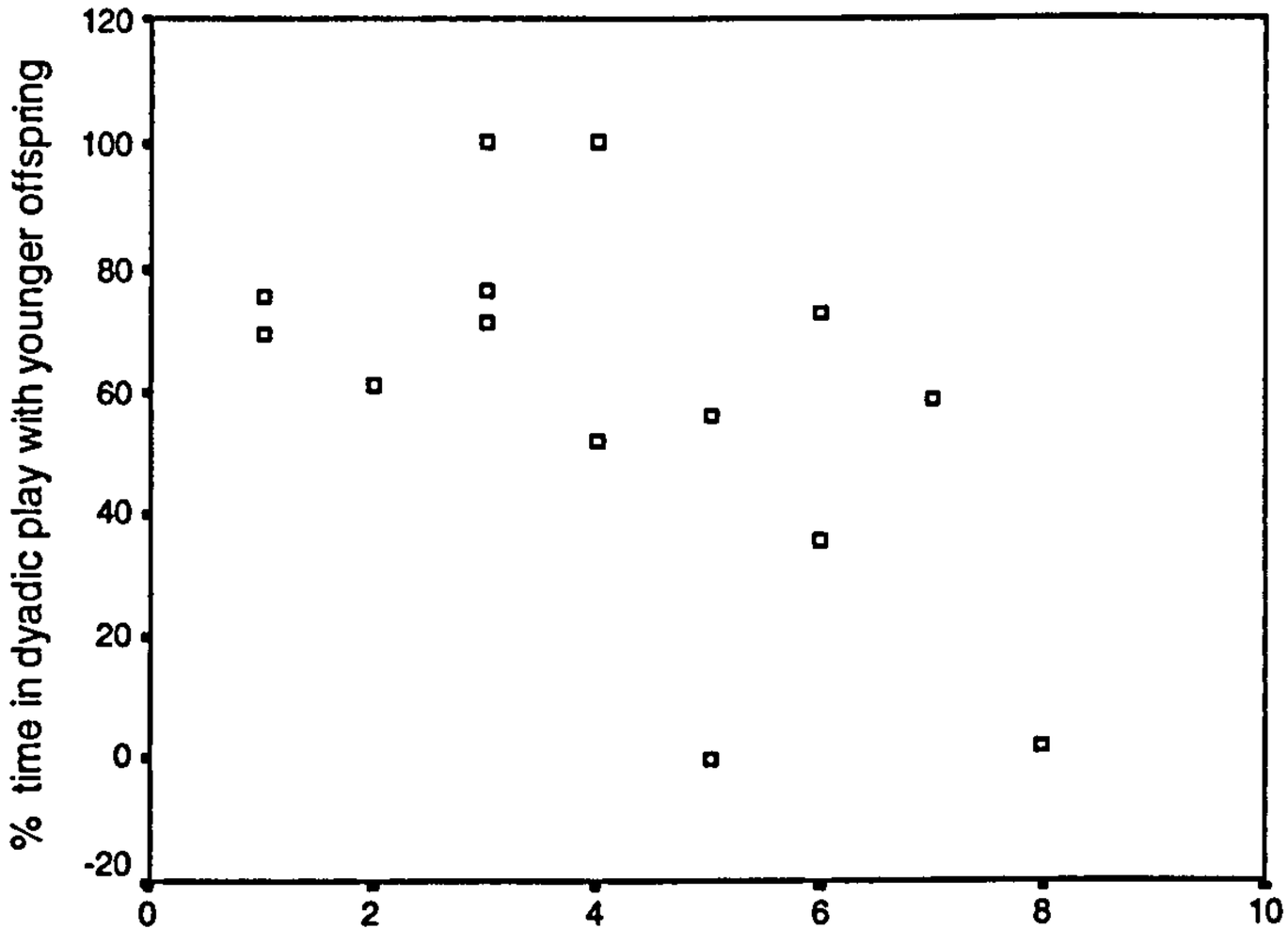


Figure 3: Scatter plot of the relative rank of the mother against the proportion of social dyadic play spent with younger offspring. Here the highest-ranking female has a relative rank of 1 and the lowest-ranking female, a relative rank of 8.

4.3.3 Aggressive, Rough and Dominance-Related Behaviour during Social Play

Despite play's fun element, coercive incidents occur at much higher rates within the social play context then in any other context. There are several contextual types of aggression that are age specific. Mothers can behave both rejecting and aggressively towards their infants over the period of weaning, at times when the infant wishes to suckle or when the infant wishes to hitch a ride on his mother's back. Adolescent males can behave aggressively towards adult females or groups of adult and adolescent females as they begin to assert dominance, and respond to the presence of adult males with quasi-

aggressive behaviours. The only non-age specific context where coercion between dependent offspring occurs, other than during play, is the feeding context. Coercion involving dependent offspring in the feeding context, excluding begging encounters between infants and mothers, which rarely results in aggression, occurred at a rate of 0.00535 interactions per focal minute. In contrast, coercive incidents involving dependent offspring in the social play context occurred at a rate of 0.043 interactions per focal minute, eight times the rate as that in the feeding context. Hence coercive incidents appear to occur at much higher rates in the play context then in other contexts, and there is an extremely significant correlation between rates of social play and rates of coercion in social play (Spearman's rho = 0.779; n = 15; p = 0.001, 2-tailed) shown in figure 4.

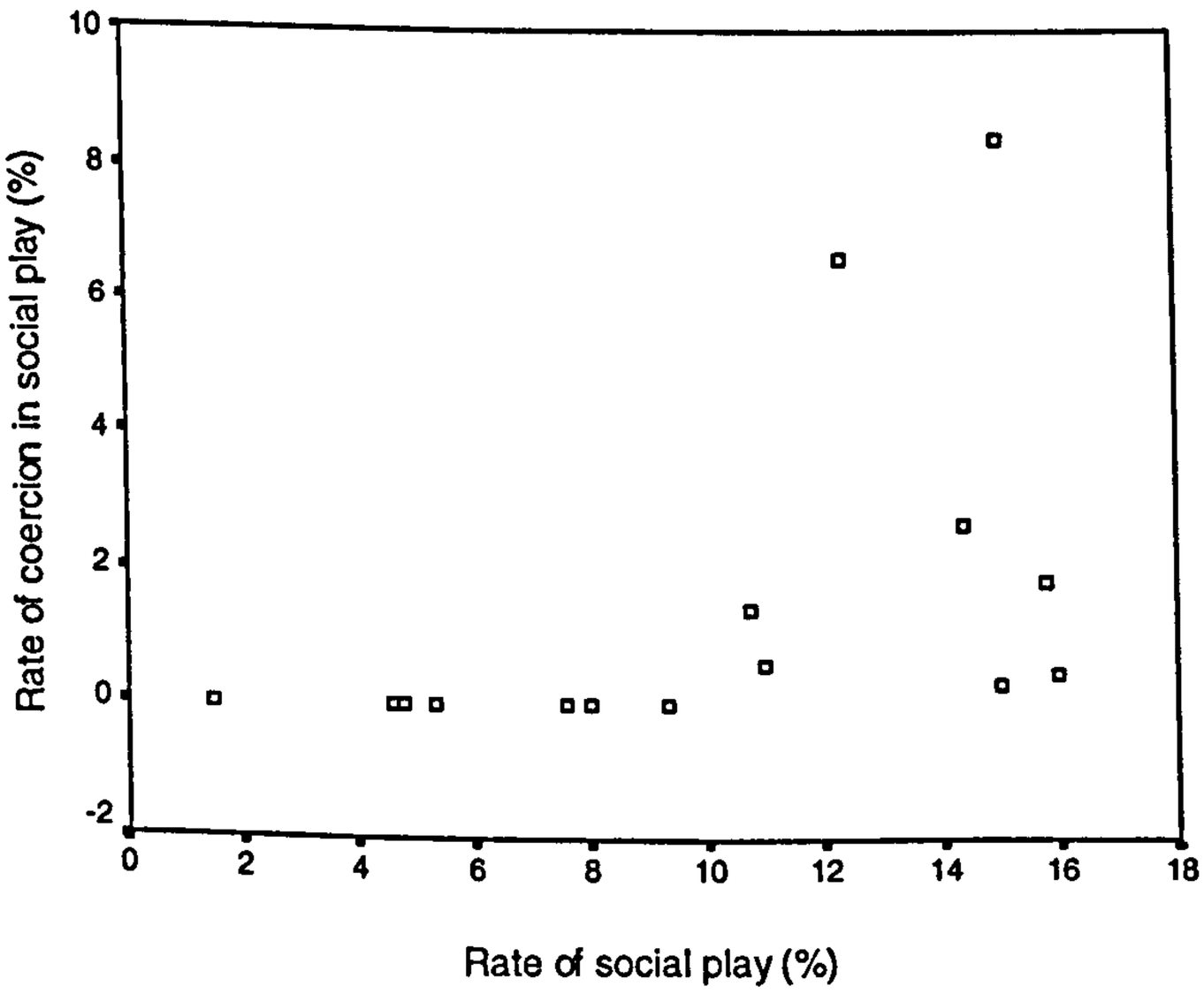


Figure 4: *Scatter plot showing a positive correlation between rates of social play and rates of coercion in the social play context, expressed as percentages, for 15 subjects.*

Dependent offspring who socially played at higher rates also used coercion at higher rates. In light of the findings that play is competitive and players appear to "play to win,"

this may not be so surprising. However, aggression in the play context deserves more attention, since it appears more chronic and widespread than in other contexts. Although chapter three found no difference between the sexes in the absolute time allocated to social play, I investigated whether a difference existed in terms of the proportion of social time allocated to social play. Social time was defined as the time spent in social behaviours, i.e. grooming and play behaviours. Since infants rarely groom, just juveniles and adolescent dependent offspring were considered in this part of the analysis (n = 4 male; n = 2 female). There was a weak trend for males to spend a greater proportion of their social time in social play than females (Mann-Whitney U = 0.00; n1 = 4 males, n2 = 2 females; $p<0.15$, 2-tailed) but no trend for these males to spend a greater proportion of their social time in social play than in grooming (Wilcoxon signed ranks T+ = 9; n = 4; $p> 0.05$, 2-tailed). There was likewise a weak trend for females to spend a greater proportion of their social time in grooming behaviours than males (Mann-Whitney Z = - 1.852; n = 4 males, n2 = 2 females; $p<0.15$, 2-tailed) but no trend for these females to spend a greater proportion of their social time grooming (Wilcoxon signed ranks T+ = 9; n=2; $p>0.05$, 2-tailed). The results are shown in figure 5 and despite apparent differences, the tests did not reach statistical significance, probably because sample sizes were too small. However the results point to a trend that could be significant in larger samples.

In 1060 focal minutes of social play between males, there were 58 minutes involving coercive (rough, aggressive or dominance related) incidents, at a rate of 0.0547 incidents per minute. In 631 focal minutes of social play between females there were 13 minutes

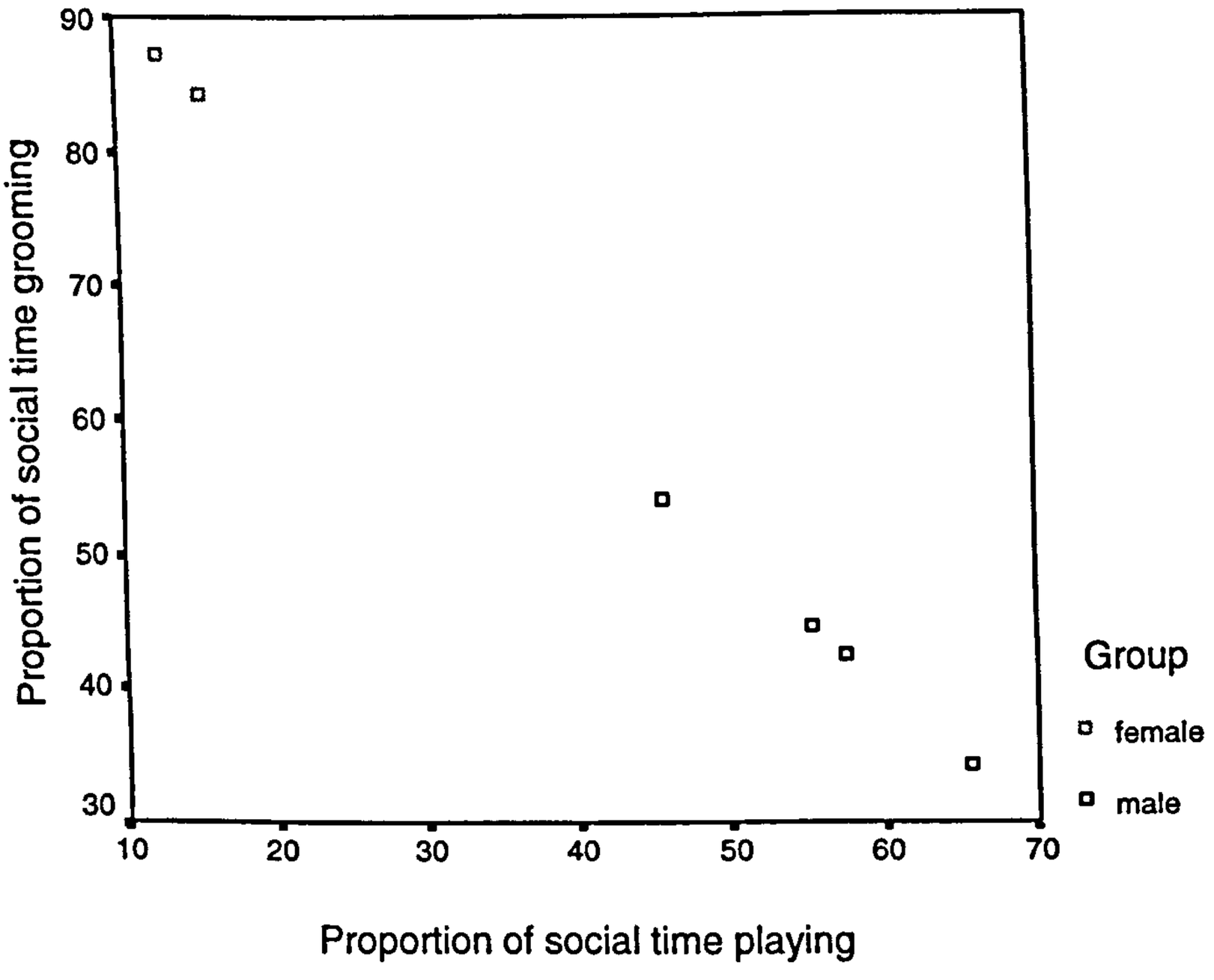
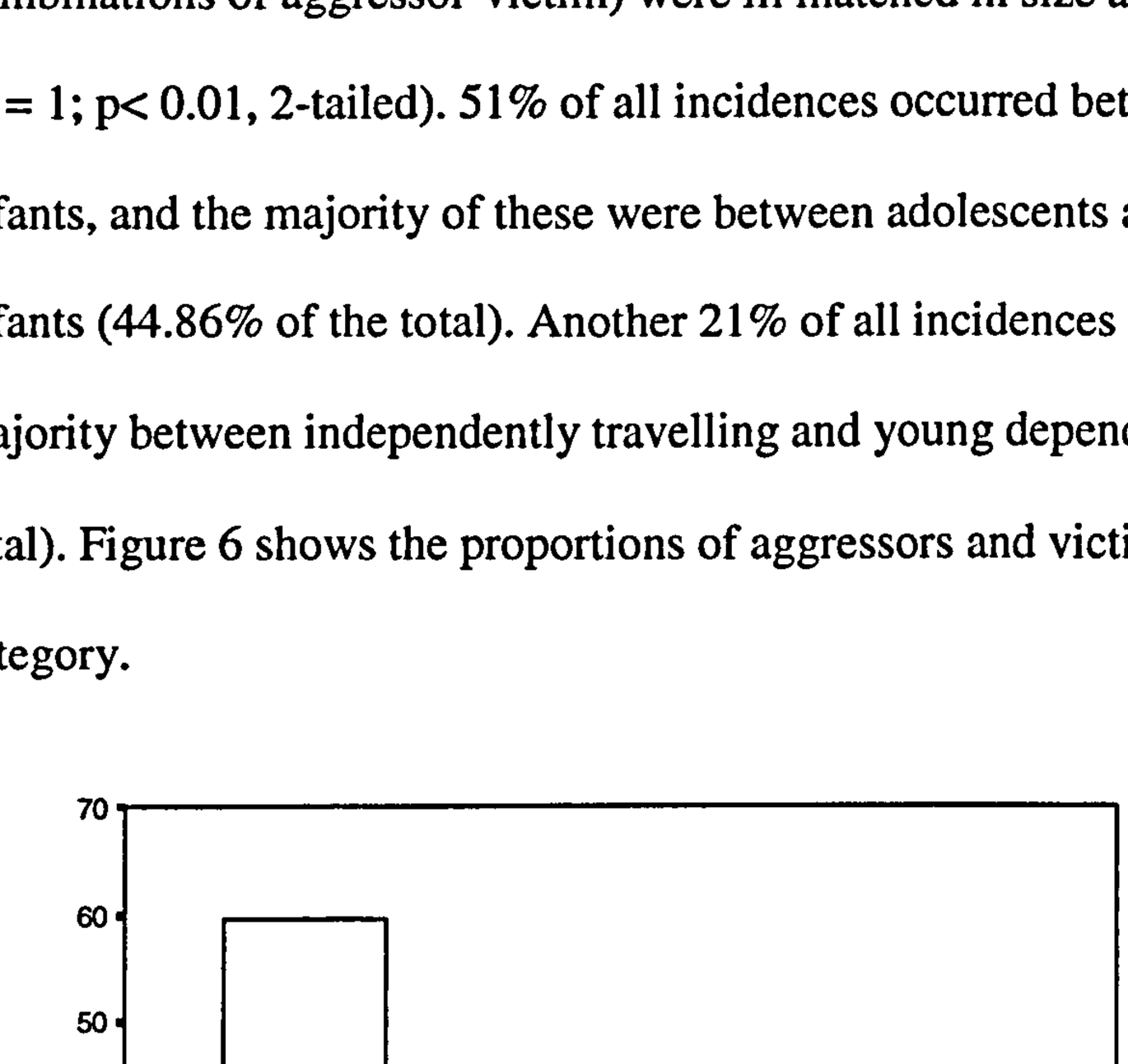


Figure 5: Scatter plot showing the proportion of social time spent playing against that spent grooming. As the plot illustrates males spend more time playing and proportionally little time grooming, while for females the reverse is true.

involving coercive incidents between females, at a rate of 0.0206 incidents per minutes. In 1697 focal minutes of social play in mixed playgroups there were 54 minutes involving coercive incidents between a male and a female, at a rate of 0.0318 incidents per minute. Coercion during social play between males occurred at more than twice the rate of that between females.

In 147 videoed incidents observed during social play, 59 were labelled as aggressive, 69 as rough and 14 dominance related. Five more incidents could not be properly described. In 51 of these incidents, between mixed dyads, the aggressor was significantly more likely to be male (chi-squared = 10.37; df = 1; $p < 0.01$, 2-tailed). The older play partner

of a dyad was more likely to be the aggressor (chi-squared = 62.06; df = 1; $p < 0.0001$, 2-tailed) as was the larger (chi-squared = 80.83; df = 1; $p < 0.0001$, 2-tailed), with size being even more significantly related to aggression than age. Consequently, significantly more coercive incidents (n = 114) occurred between ill matched pairs than between well-matched pairs (chi-squared = 29.5; df = 1; $p < 0.001$, 2-tailed) and significantly more dyads involved in coercive incidents (n = 49 different dyads in n = 52 different combinations of aggressor-victim) were ill matched in size and age (chi-squared = 9.31; df = 1; $p < 0.01$, 2-tailed). 51% of all incidences occurred between adolescents and infants, and the majority of these were between adolescents and independently travelling infants (44.86% of the total). Another 21% of all incidences were between infants, the majority between independently travelling and young dependent infants (13.16% of the total). Figure 6 shows the proportions of aggressors and victims falling into each age category.



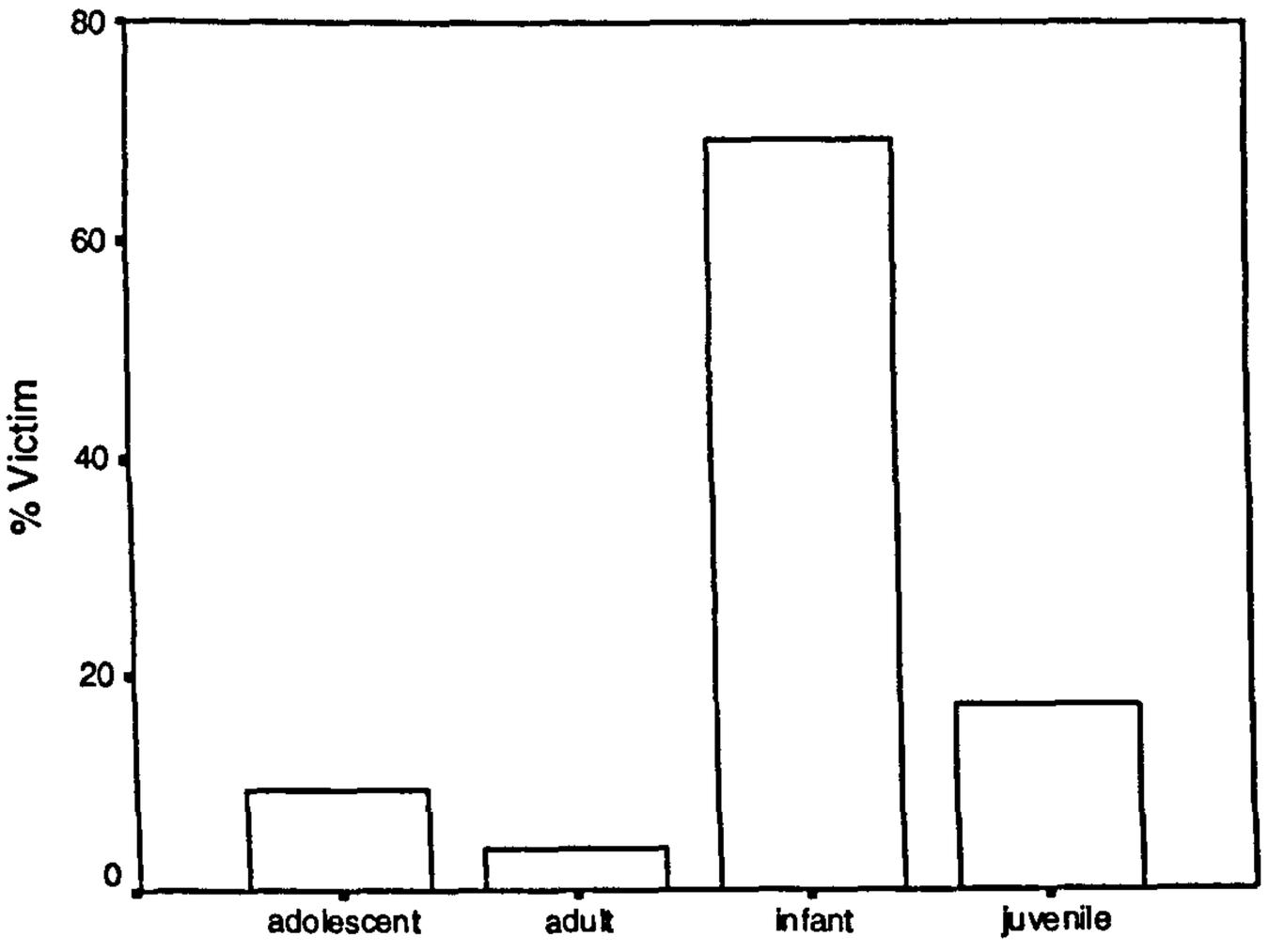


Figure 6: Two bar charts showing the percentage of aggressors or victims falling into each age category, in 52 different dyadic combinations of aggressor-victim, during videoed dyadic social play.

In 114 videoed incidents of rough, aggressive or dominance-related behaviours during social play, where the degree of relatedness was known, 50 incidents were between an unrelated dyad, 40 incidents occurred between siblings and 24 incidents occurred between dyads related by $r = 0.125$. There was a significant association between the degree of relatedness and occurrence of such incidents. Incidents occurred between unrelated dyads significantly greater than by chance (chi-squared = 9.05; df = 2; $p < 0.02$, 2-tailed). In 49 different dyads showing rough, aggressive or dominance-related behaviours during dyadic play, significantly more of the unrelated dyads (n = 35), interacted roughly or aggressively than the related dyads (n = 14), (chi-squared = 9; df = 1; $p < 0.01$, 2-tailed).

4.3.4 Aggression and Play

Assuming that all incidents recorded as rough were unintentional, it becomes obvious why rough play occurs predominantly among ill matched pairs. The largest and strongest can, in the excitement of physical but playful combat, exert his or herself just enough to unintentionally hurt a younger play partner. There are difficulties in assigning rough incidents as intentionally aggressive, since the vocal response of the victim appears to keep in check the actions of the so called "aggressor," so play resumes and no more negative actions are taken against the victim. Similarly, it is just as possible that rough incidents are intentionally aggressive, since chimpanzees appear to "play to win" and such incidents could be a strategy to meet this goal. Because of this dilemma in interpreting this kind of behaviour, I decided to analyse behaviour that was clearly aggressive separately, in order to confirm the above results, omitting other coercive behaviours that could be classed as rough or dominance related.

Aggressive behaviour between males occurred at a rate of 0.0198 incidents per focal minute of social play involving just males. Aggressive behaviour between females occurred at a rate of 0.00475 incidents per focal minute of social play involving females. Hence, aggression between males occurred at four times the rate as that between females. There were 51 well observed videoed incidents of aggression. Again the aggressor was significantly more likely to be male than female (chi-squared = 17.3; df = 1; $p < 0.0001$, 2-tailed) in aggressive incidents involving both sexes. In 37 different dyadic combinations of aggressor-victim, again both the older and larger play partner was more likely to be the aggressor (chi-squared = 9.3; df = 1; $p < 0.01$, 2-tailed; chi-squared =

11.57; df = 1; p <0.001, 2-tailed, older and larger respectively). In 51 videoed aggressive incidents where both aggressor and victim were known, significantly more aggressive incidents occurred between ill matched pairs than between matched dyads (chi-squared = 18.84; df = 1; p < 0.0001, 2-tailed) and 51% occurred within dyads composed of an adolescent aggressor and an infant victim. Out of 33 different aggressor-victim dyads involved in the aggressive incidents significantly more were ill matched than well matched (chi-squared = 6.82; df = 1; p<0.01, 2-tailed, where all infants are grouped together; chi-squared = 13.36; df = 1; p < 0.001, 2-tailed where independent travelling infants are differentiated from younger infants) and over 72% of the dyads involved an adolescent aggressor.

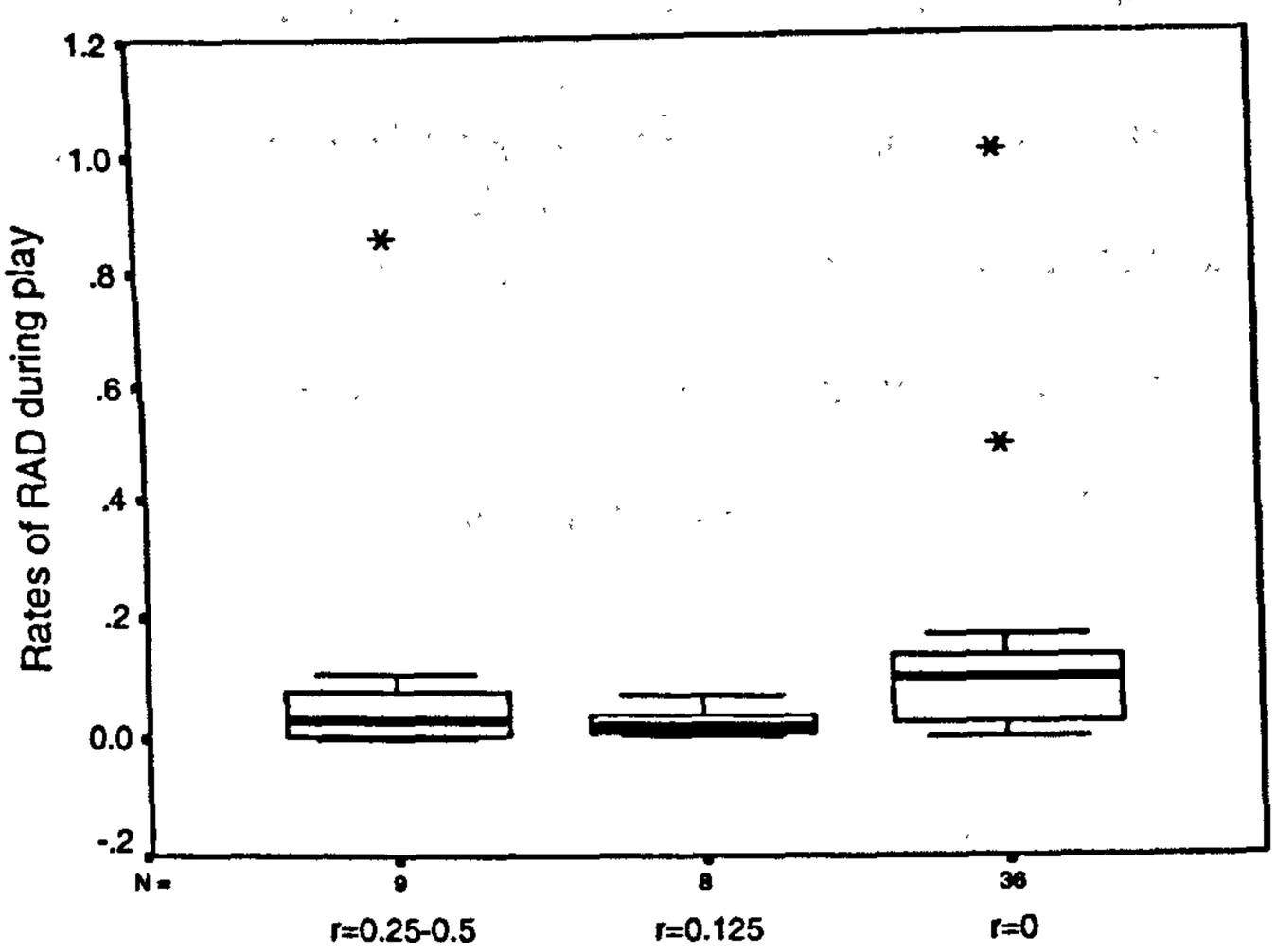
Out of 29 video recorded dyads involved in aggressive incidents, where the degree of relatedness was known, 20 were unrelated, 3 were related by r = 0.125 and 6 were related by r = 0.25-0.5. There was a significant association between degree of relatedness and the occurrence of aggression (chi-squared = 17.04; df = 2; p< 0.001, 2-tailed). Aggression between unrelated dyads occurred at the greatest frequency while aggression between dyads related by r = 0.125 occurred at the lowest frequency. However aggression between dyads more closely related (r = 0.25-0.5) occurred at a frequency closest to chance, suggesting the significant effects were mainly attributable to dyads that were less closely related.

In summary, aggression between males, in the social play context occurred at a much higher rate than that between females. Aggressive incidents occurring between mixed

dyads were more likely to be instigated by the male play partner, than the female partner. The aggressor was also more likely to be the older and larger play partner in a dyad, and was more likely to be an adolescent, among the videoed play bouts, at least. Aggression was more likely to occur between ill matched play partners, with regards to age and size, and among pairs of individuals who were maternally unrelated.

4.3.5 Rates of Aggression and Relatedness

The following section analyses rates of coercion (aggression, rough and dominance incidents) between different aggressor-victim dyads, using data from focal follows. Complementing the above findings, there was a significant difference in the rates of aggressive, rough and dominance incidents (RAD), aggressive and rough incidents (RA), and aggressive incidents (A) and the degree of relatedness between dyads (RAD: Kruskall-Wallis chi-squared = 9.190; df = 2; n = 53 dyads; p =0.01, 2-tailed; RA: Kruskall-Wallis chi-squared = 7.396; df = 2; n = 48 dyads; $p < 0.05$, 2-tailed; A: Kruskall-Wallis chi-squared = 8.538; df = 2; n = 28; $p< 0.05$, 2-tailed). Rates between members of a dyad were affected by their degree of relatedness. Figure 7 shows this relationship for both RAD and A. RAD, RA and A occurred at significantly higher rates among unrelated dyads than between related dyads (RAD: Mann-Whitney U = 149; n1 = 17 related, n2 = 36 unrelated; $p <0.01$, 2-tailed; RA: Mann-Whitney U = 114.5; n = 48; $p<0.01$, 2-tailed; A: Mann-Whitney U = 23; n1 = 8 related, n2 = 20 unrelated; $p<0.005$, 2-tailed). Coercion was therefore more likely to occur between unrelated dyads than between related dyads, supporting findings from the videoed play bouts. Figure 8 shows this relationship in graphical form.



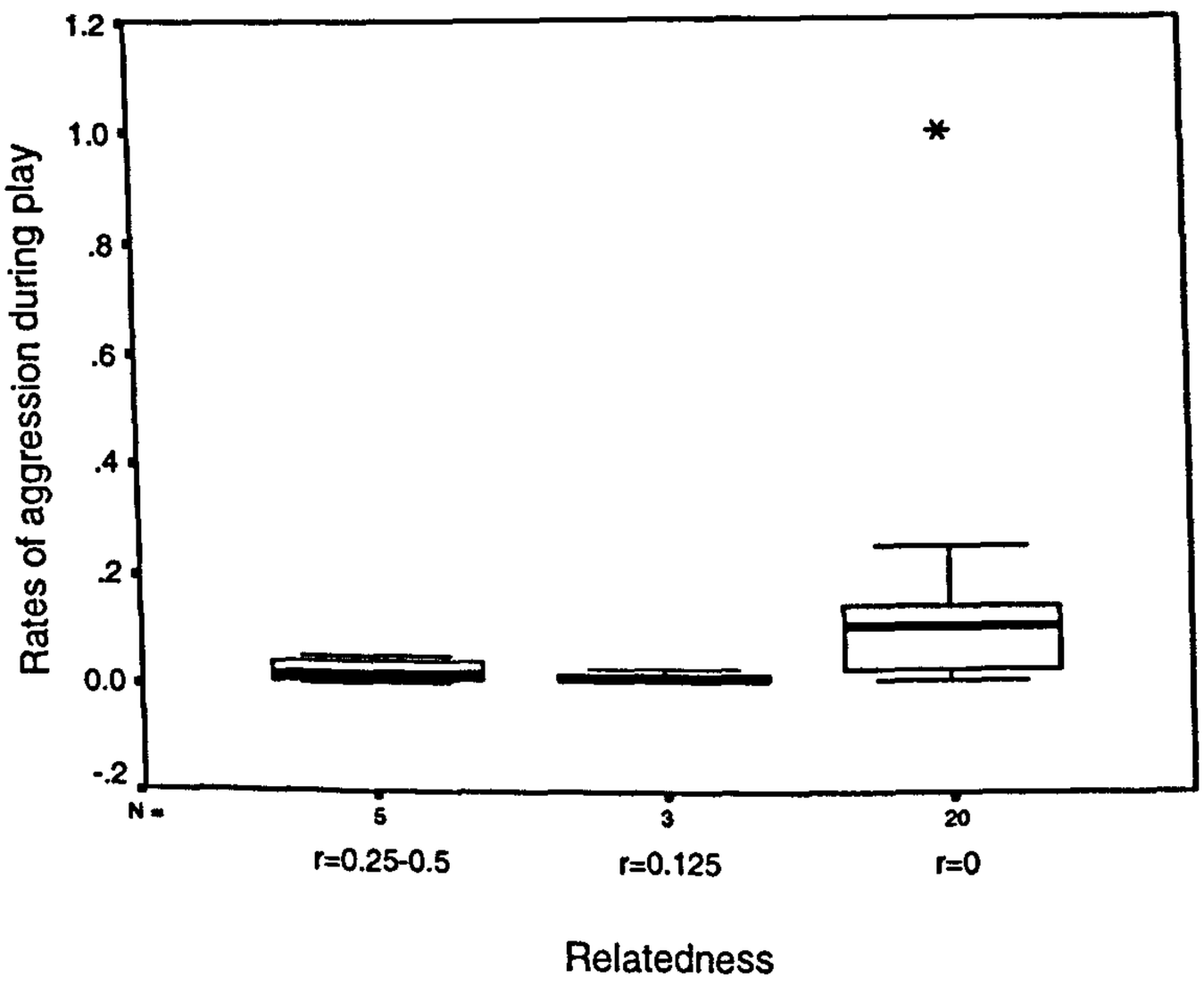


Figure7: Two box plots showing median rates of RAD (rough, aggressive and dominance incidents) and median rates of aggressive incidents, between dyads, grouped by their degree of relatedness (r=0 unrelated; r=0.125 nephew, uncle etc; r=0.25-0.5 sibling). Each plot shows the median, quartiles and extreme values in each category.

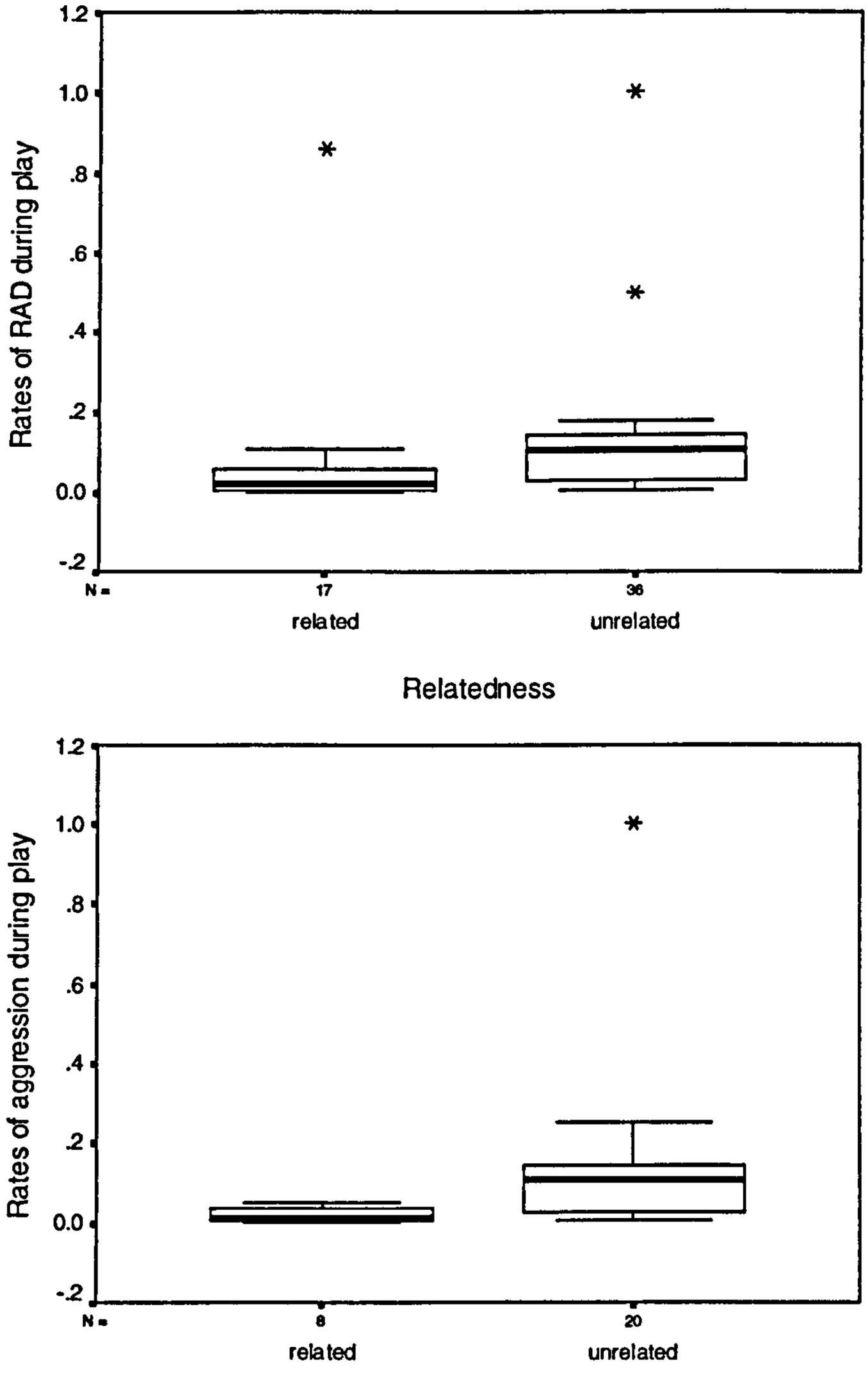
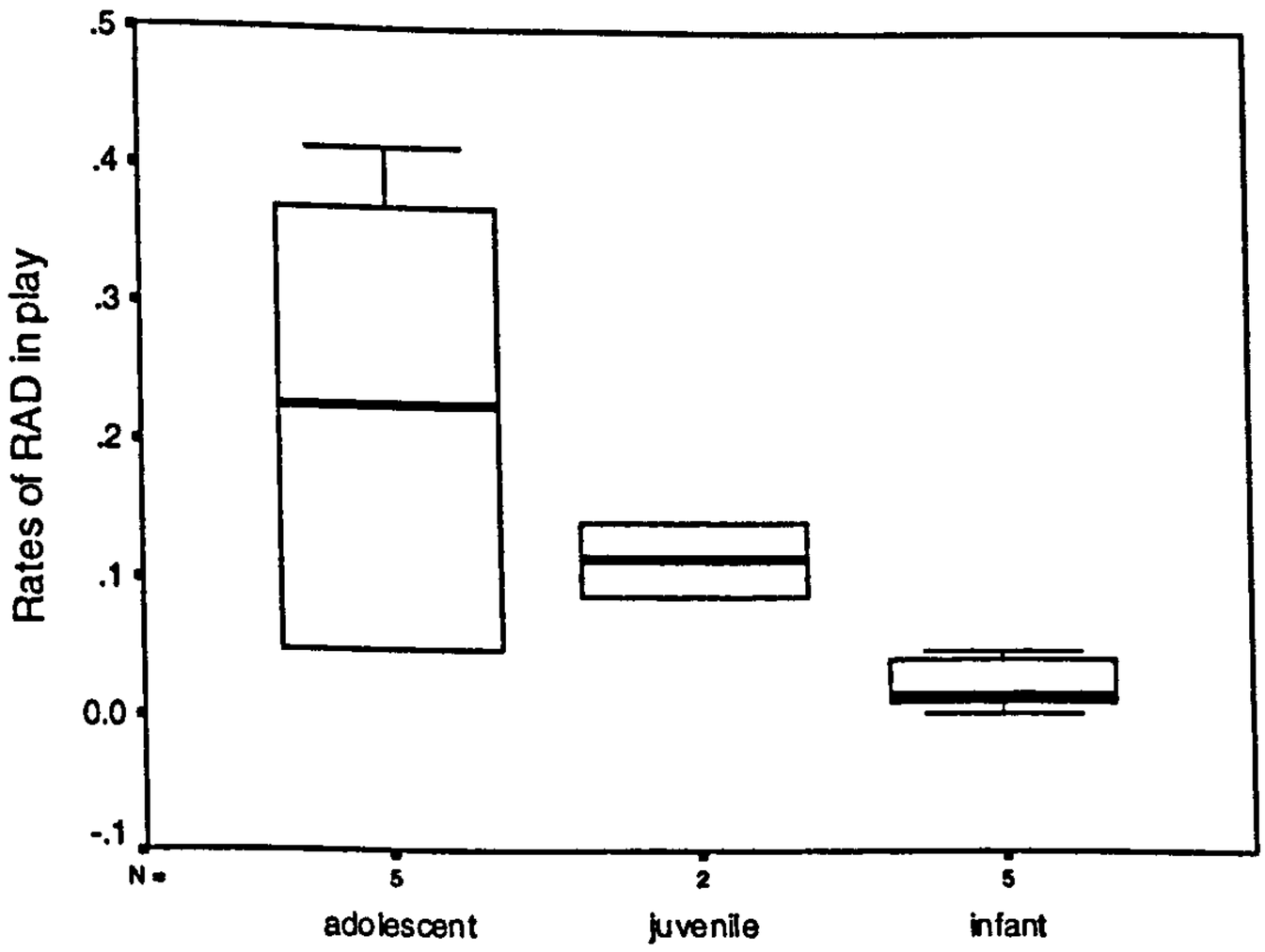


Figure8: Box-plots showing the median rates of RAD (rough, aggressive and dominance incidents) and median rates of aggression between related and unrelated dyads, in dyadic social play. Each plot shows the median, quartiles and extreme values within a category.

There was a tendency for rates of RAD and A to be higher between ill matched pairs than between matched pairs (RAD: Mann-Whitney U = 5; n = 15 dyads; $p < 0.1$, 2-tailed; A: Mann-Whitney U = 8; n = 11 dyads; $p < 0.1$, 2-tailed), although this did not reach significance. This suggests that although the number of videoed coercive incidents

observed between ill matched pairs was significantly greater than between well-matched pairs, ill matched pairs played more often together. There was however a significant difference between adolescents, juveniles and infants in the rates of RAD, RA and A performed. Adolescents performed these behaviours at the greatest rates and infants at the lowest. Adolescents and juveniles performed at higher rates than infants (RAD: Kruskall-Wallis chi-squared = 6.246; df = 2; n = 12; $p < 0.05$, 2-tailed; RA: Kruskall-Wallis chi-squared = 6.033; df = 2; n = 10; $p < 0.05$, 2-tailed; A: Kruskall-Wallis chi-squared = 7.208; df = 2; n = 12; $p<0.05$, 2-tailed). These results are shown graphically in figure 9. There was however no significant difference in rates of aggressive behaviours received during play between adolescents, juveniles and infants (RAD: Kruskall-Wallis chi-squared = 3.293; df = 2; n = 14; $p>0.05$, 2-tailed; RA: Kruskall-Wallis chi-squared = 4.934; df = 2; n =13; $p<0.1$, 2-tailed; A: Kruskall-Wallis chi-squared = 0.727; df = 2; n = 10; $p> 0.05$, 2-tailed), although there was a trend for rates of aggressive and rough incidents (RA) to be lower towards juveniles than to other age classes. This suggests that despite the fact that a large percentage of incidents recorded on video involved an infant as a victim, dyads composed of at least one infant were observed to play more in the videoed play bouts.



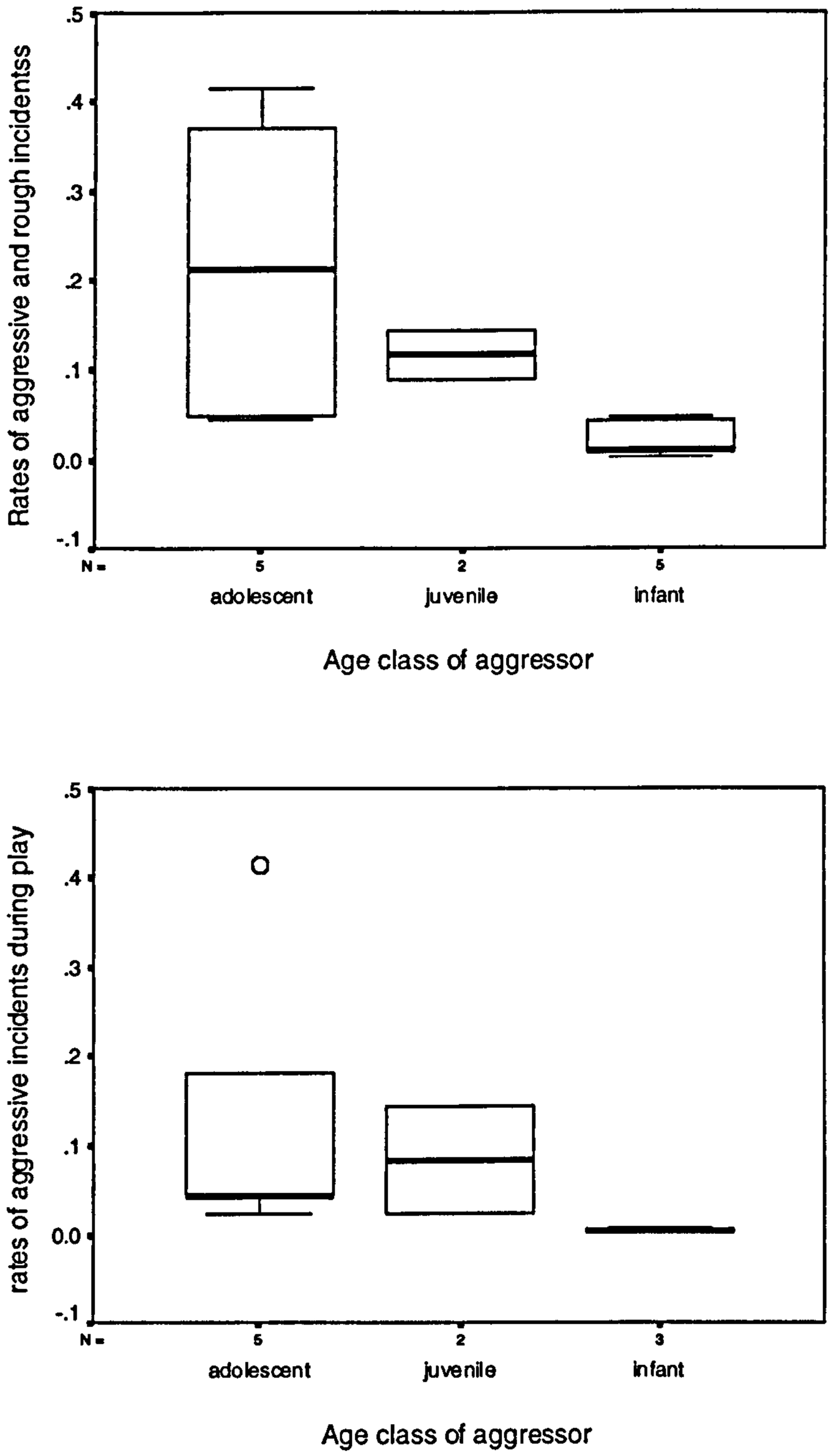


Figure 9: Box plot showing the median rates of RAD (rough, aggressive and dominance incidents), RA (rough and aggressive incidents), and aggressive incidents during play for three different aggressors: adolescents, juveniles and infants. Each plot shows the median, quartiles and outliers within a category.

There was a significant negative correlation between the rates of RAD, RA and A given by a focal to his play partner and the social play frequency of that dyad (see chapter three for a definition of social play frequency). As rates of play between dyads increased, rates of RAD decreased significantly, showing that dyads that associated most often showed the least antagonism towards each other (RAD: Spearman's rho = -0.433; n = 33; p <0.05, 2-tailed). This is shown in figure 10. For rates of RA and A there was a significant tendency for this to be the case (RA and A: Spearman's rho = -0.444; n = 16; p<0.1, 2-tailed).

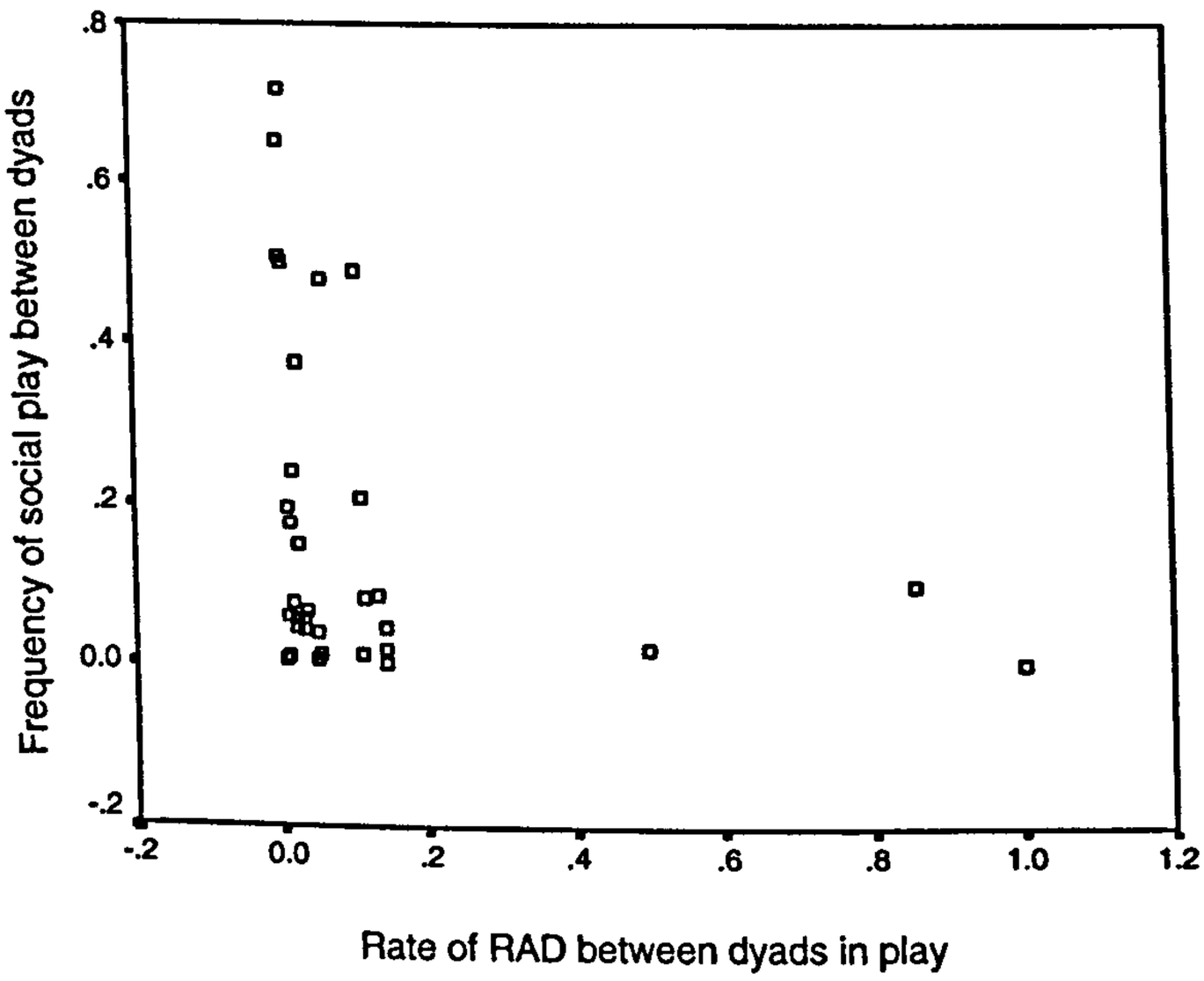


Figure 10: Frequency of social play between a dyad against the frequency of rough, aggressive and dominance related incidents occurring between the same dyad. Social play frequency was calculated as the amount of time the focal (the aggressor) spent playing with play partner as a proportion of the total time spent in social play.

4.3.6 Responses to Aggression: Maternal and Third Party Response/Intervention

In the following two sections, I describe in detail the behavioural responses to coercion in the play context by different parties. Because these behavioural responses were not

always described in detail, sample sizes are small. However some patterns were identified, providing a basis for future research.

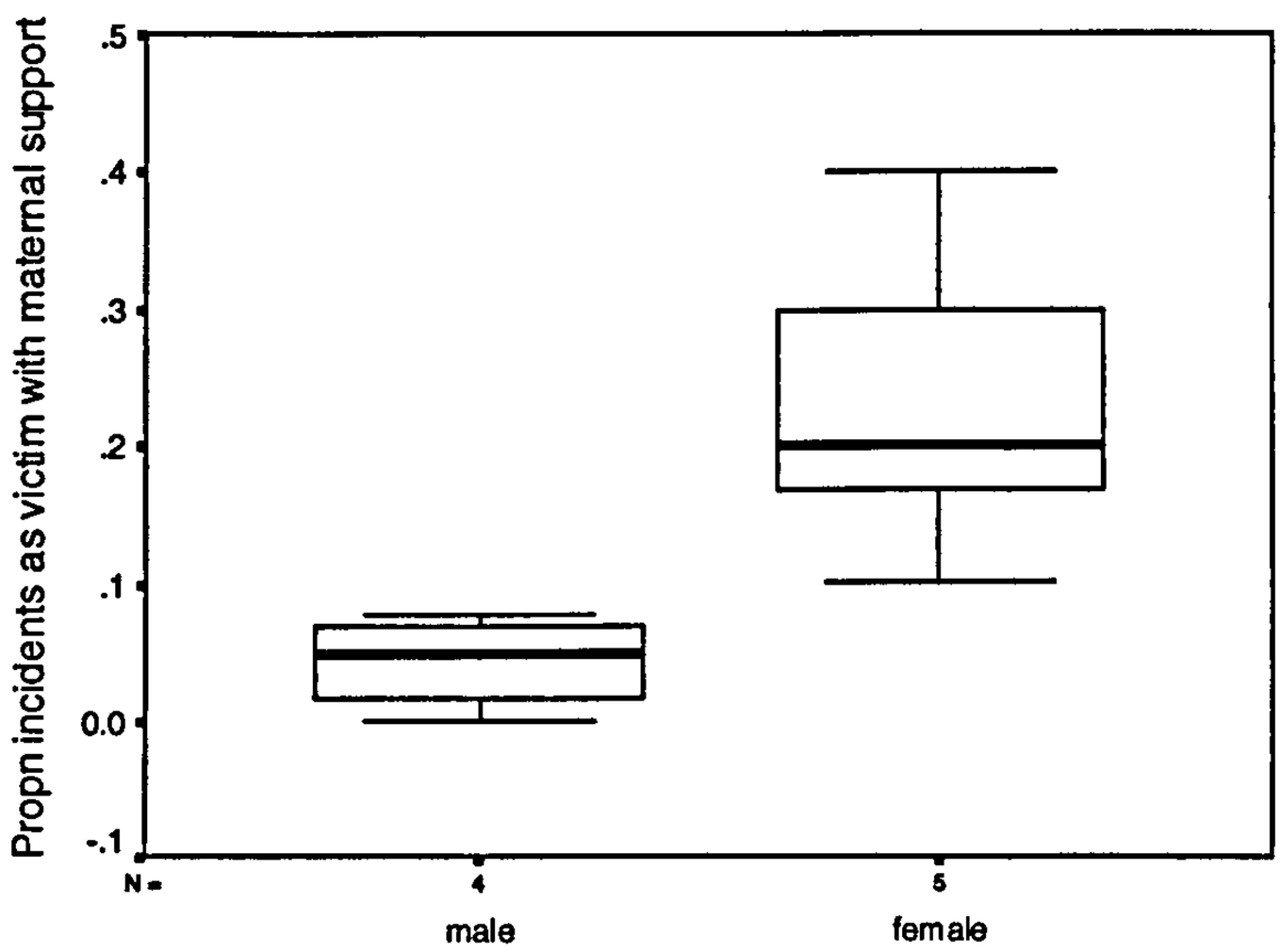
Out of 83 incidents (from focal follows) where response to coercion was recorded in detail, in 19% of the cases (n = 16) the mother of the victim was seen to respond. In 14 out of 15 of the 16 incidents, where the victim was identified, the victim was an infant, suggesting that maternal response may be exclusively given to infants in the play context. Responses could be classed into four types of behaviours: maternal retaliation (e.g. threat) in support of offspring, retrieve offspring, approach offspring, or contact offspring. In three incidents (18.75%), the mother threatened the aggressor (the most severe response observed), and in all three cases the aggressor was unrelated to both the mother and the victim. In five incidents (31.25%), the mother retrieved the infant, pulling the infant to her ventrally in a defensive manner. In four out of these five cases the infant was still dependent on its mother for travel, and in the fifth case, where the victim was an independently travelling infant the aggressive incident was particularly severe. Therefore retrieval may be a behavioural response confined to very young infants or severe conflicts. The degree of relatedness between aggressor and victim, averaged across all five incidents was r =0.0625 and in three out of the five incidents the aggressor and victim were unrelated. Maternal approach without making contact may be a defensive strategy used by mothers towards older infants who are not in immediate proximity, since in all incidents (n = 4) the victims were independently travelling infants. Mothers may prefer not to intervene directly if they are confident that their offspring can defend themselves adequately, but remain vigilant just in case conflicts escalate. Again the

degree of relatedness averaged across all incidents was r=0.0625 with three out of four victims being unrelated to their aggressors. Finally, in four cases, the mother made comfort-contact with the victim, involving grooming, presenting her back in order to be hugged, touching or stroking behaviours. The degree of relatedness, averaged across all four cases was the highest in any response group with an average of r=0.15625. In three out of four cases the aggressor was a relative.

Although the sample size of incidents is small the data indicates that maternal response to coercion in the play context appears dependent upon both the age of the victim and the degree of relatedness between victim and aggressor. The most severe responses were given to individuals who were unrelated, whereas, arguably, the least severe response (offering comfort) occurred most often in cases where the victim and thus the mother were related to the aggressor.

Figure 11 shows two box-plots showing the proportion of coercive incidents supported by the mother for each male and female infant. The first box-plot regards each coercive incident as independent. The second regards each play session with an aggressive or rough incident as independent. All infants were included along with one juvenile male (Fudge) who was just over 5 years of age half way through the study, but who had a younger brother, had been weaned early and therefore was regarded as a juvenile. In both cases, mothers intervened significantly more often in coercive incidents for victimised infant daughters than for victimised infant sons (where each incident regarded as independent: Mann-Whitney $U = 0; n = 9$; $p<0.05$, 2-tailed; where each play session as

independent: Mann-Whitney U = 1; n = 9; $p<0.05$, 2-tailed). One reason for this female bias in maternal intervention might be proximity factors; if female infants keep closer proximity to their mother during social play then mothers may be more likely to detect conflicts visually and react to them in a defensive manner sooner. Although there is no real reason to suspect a difference, I investigated this point simply by averaging the distance between male offspring and their mothers, and female offspring and their mothers, just prior to the coercive interaction. Distances were marked by 1 =



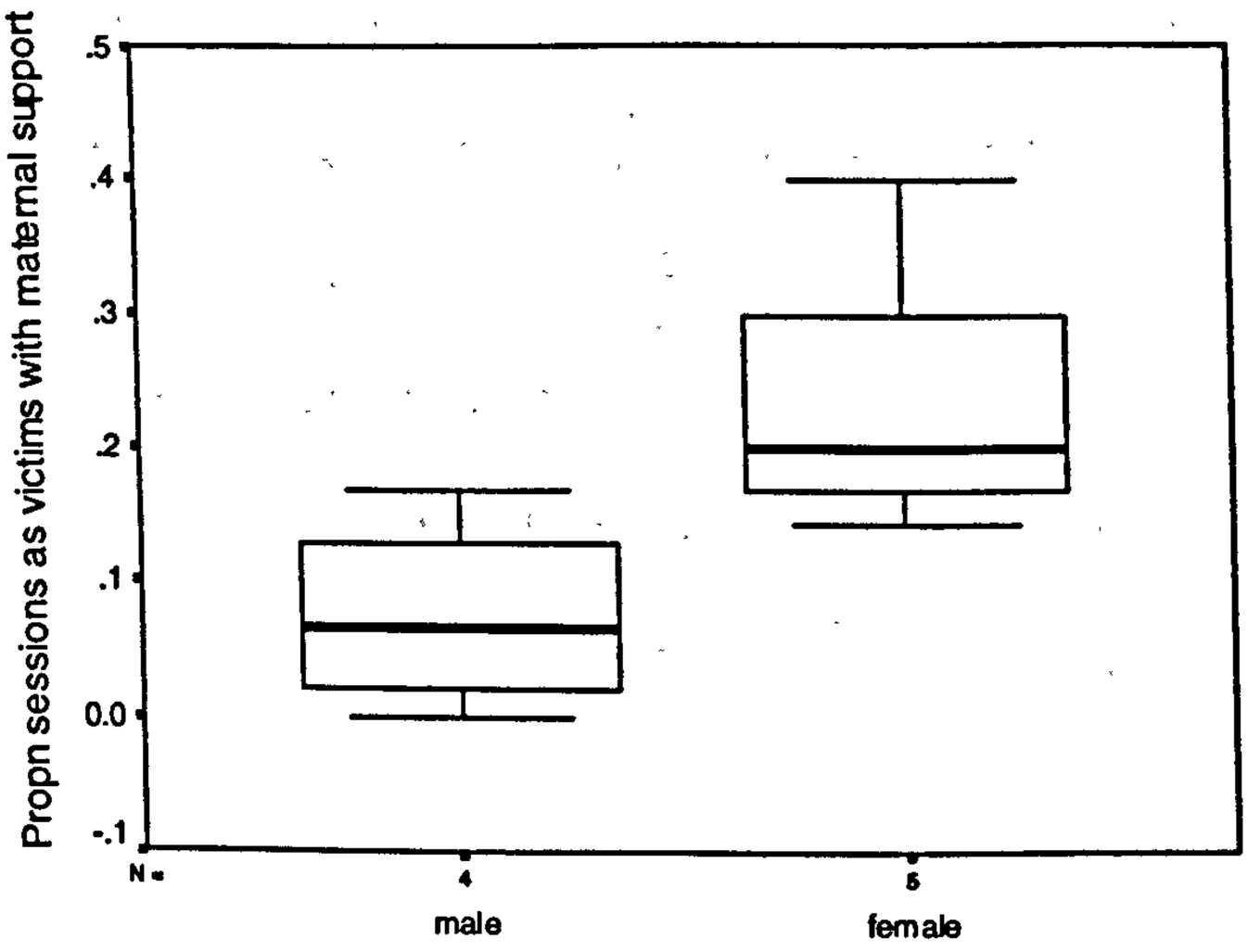


Figure 11: 1. Box-plot showing the proportion of aggressive/rough incidents, where the mother of the victim intervenes, or supports her offspring, for male and female infants. 2. Box-plot showing the proportion of play sessions with aggressive/rough incidents where the mother of the victim intervenes or supports her offspring for male and female infants.

touch, 2 = arm's reach, 3 = 1-5 metres etc. Averaging these ordinal values across male and female offspring separately, I found that the average distance between a male offspring and his mother during such incidents was 2.75, i.e. between arm's reach and five metres, whereas for females the average distance gave a value of 3.0975 or betweer one and five metres. Although male victims appeared to be in disputes at, on average, slightly shorter distances from their mothers than female victims, and hence one could alternatively argue that the closer proximity of the mother precludes intervention, the difference was too small to convincingly explain maternal bias in support of female offspring in terms of proximity.

In a further 12 incidents, a third party, other than the mother of the victim, intervened. In the two cases where a third party retaliated aggressively on behalf of the victim, both were adolescent siblings of the victim (r = 0.25-0.5) and in one case the nephew of the victim (r = 0.125) approached the aggressor and threatened him by flicking his wrist. In two further cases, a nephew or uncle (r = 0.125) of the victim responded to the aggression by initiating play or joining in the session between aggressor and victim. Either the aggression appeared attractive, or resumption of play by a third party distracted the victim or the aggressor away from the conflict, thus ending the incident. In four cases, another play partner reassured or consoled the victim. In three out of the four cases, the consoler was also a sibling of the aggressor. In the one case where this was not the case, the aggressor responded by retaliating against the consoler, suggesting that consolation may carry risks for those individuals who are unrelated to the aggressor. In one incident, the mother of the aggressor pulled the aggressor to her away from the victim, but in this case she was also the grandmother of the victim. Finally, in just two incidents, two unrelated females to either party appeared to respond to the conflict by approaching it, where in one case the aggressor responded in turn by initiating play with the female.

4.3.7 Response of the Aggressor and Victim Beyond the Aggressive Act.

In seven out of 15 incidents where the response of the aggressor was noted in detail beyond the aggressive act, the aggressor responded by moving off or running away from the victim. In six out of seven of these incidents, the victim and aggressor were unrelated. Conversely in a further seven incidents, the aggressor actively restrained or held the victim ventrally for consolation. The average degree of relatedness of this group was

higher, with four out of seven of the victims being either a sibling (r = 0.25-0.5) or another relative (r = 0.125). This suggests that the response of the aggressor beyond the aggressive act may depend upon the degree to which he is related to or familiar with the victim.

In 25 out of 52 incidents (48%) where the response of the victim was noted in detail, the victim approached or made contact with his/her mother. In a further five cases (8.5%), the victim approached another relative or another play partner other than the aggressor. In 12 incidents (23%), the victim simply moved away from the aggressor. The victim retaliated in six incidents; half of such incidents occurred between siblings and half between unrelated individuals. In seven incidents (13.5%), the victim approached the aggressor or actively reconciled with him by restraining and presenting to or holding the aggressor. Again in half of these cases the aggressor and victim were related and half were unrelated, suggesting that in the case of the victim, retaliation and reconciliation may depend more on other factors than upon the degree to which two individuals are related, such as the proximity of relatives, for instance.

In summary, responses to aggressive incidents among dependent offspring by third parties, depends upon the degree of relatedness between them and the victim or the aggressor. The available data suggests that the strength of a response given by a mother of a victim depends upon the degree of relatedness between the aggressor and victim/victim's mother. Furthermore, rates of victim support by the victim's mother, among infant victims at least, are also dependent upon the sex of the victim, with mothers

supporting their infant daughters more than their infant sons during conflicts. The data also indicates that the strength of response by other third parties intervening on behalf of the victim may also depend upon on the degree of relatedness between the third party and the victim or the aggressor. In all cases where a third party retaliated on behalf of the victim, with overt forms of aggression toward the aggressor, the third party was the victim's sibling. Furthermore, consolation towards a victim may be a behavioural response most commonly employed by a relative of the aggressor, since support by non-relatives may incite further aggression. Finally the response of the aggressor to the victim may also depend upon their degree of relatedness, since aggressors showed a greater tendency to console victims to whom they were related. Although the data are sparse, these results illustrate the importance of having relatives present at times of conflict, from an early age. Since conflicts arise primarily in the play context, play provides an opportunity for offspring to learn whom they can rely on for support and behavioural responses related to conflict resolution.

4.4 Discussion

4.4.1 Is Play Competitive and Do Chimpanzees Play to Win?

Social play among dyads of immature chimpanzees appears to be strongly competitive as has been found in a number of other primate species (e.g. Biben 1986). Winners and losers are usually easily distinguishable, based upon postural differences and the winner's degree of control over subsequent events (Thompson 1998). Chimpanzees compete mutually for the possession of an object, for a superior position, and in the case of triads, often for possession or the attention of another individual, or a combination of those

mentioned. Motor patterns are not random but appear geared toward gaining physical advantage over the opponent. Some motor patterns can be categorised into particular games such as those used to gain the superior position during "dangle-play".

Among chimpanzees, the older and subsequently larger wins most play bouts and among dyads there is usually a large difference in size and age. Unlike many other species, chimpanzees do not play most frequently with well-matched partners (Siberian ibex *Capra ibex siberica*, Byers 1977; bighorn sheep *Ovis canadensis,* Berger 1980; common marmosets *Callithix jacchus,* Stevenson & Poole 1982; squirrel monkeys *Saimiri sciureus*, Biben 1986; sable antelope *Hippotragus niger*, Thompson 1996). Biben (1986) observed that most squirrel monkey play occurred between individuals with similar probabilities of winning and play between ill matched partners was less frequent, presumably because the smaller partner was less likely to desire to play a bout with an opponent he is likely to lose against. However, chimpanzees are constrained demographically to play with individuals ill matched in age and size, whereas many of the species cited above give birth seasonally resulting in peer groups of similar aged individuals. While offspring didn't spend a greater proportion of their dyadic playtime, playing with younger offspring, there was a strong tendency for independent travelling infants to do so. A linear relationship between maternal rank and the proportion of dyadic playtime allocated to younger individuals, suggested that offspring with high-ranking mothers use strategies to maximise their probability of winning play bouts. Winning therefore appears more important to the offspring of high-ranking females. Since it was found in chapter three that offspring of high-ranking females and their adult daughters

socially play at significantly higher rates, it is possible that greater social experience leads to a greater degree of competitiveness. There are two possible but related reasons why independently travelling offspring show a tendency to spend a greater proportion of their dyadic play, playing with younger offspring, while older offspring don't. First, offspring at this age might be inhibited from playing with older offspring, if these offspring are rougher or more aggressive in their play and might therefore prefer to play younger individuals, if present. Second, at this age, offspring might be truly playing to win, while at older ages social play might function in a different way related to the establishment of dominance (see below).

Biben (1986) and Owens (1975a) observed that squirrel monkeys and baboons were more likely to initiate play with partners whom they could dominate and Thompson (1998) found for infant punares that the probability of winning was higher when the infant initiated the bout than when it was the recipient. This study shows that the younger (and smaller) play partner in a dyad initiates an approach more often. There is therefore a trend for the probability of losing being higher when the individual initiates approach, and the probability of winning being higher when the individual becomes the recipient of approach initiations. The individual initiating contact, most often in response to approach initiations but sometimes in the absence of them, is more often the winner (therefore supporting the idea that the initiator, in terms of initiating contact, is more likely to win the bout). Losers terminate more often. Social play among chimpanzees, although competitive, is one-sided, with a small probability of the younger and smaller player winning, despite the commonality of ill matched players playing together. While losers

appear motivated to terminate a bout, at the same time they appear motivated to initiate a bout they are more likely to lose. Among pairs of adult male rats, it was found that subordinates initiated more playful contacts than dominants (Pellis, Pellis & McKenna 1993) and this was explained in terms of subordinates initiating play in order to maintain familiarity and tolerance by the dominant. As chapter three demonstrated, social play among chimpanzees may function in the maintenance of social bonds and therefore winning may not be the only goal. There is a degree of ambiguity in approach initiations, in that the initiator appears to signal his motivation to play and his attraction to the older individual (who is likely to win the bout) while maintaining a distance. Perhaps because play is one-sided, the larger and stronger individual waits for a signal from the smaller individual (who is likely to lose the forth-coming bout) denoting his motivation to maintain the association, before making a definitive initiation/contact. In this sense, play initiations are reciprocal. Owens (1975a) documented the same pattern in baboons *Papio anubis,* and suggested that due to the age/size difference, the larger individual might restrain himself more. For chimpanzees, the fact that the smaller and younger partner is responsible for both initiating and terminating the play bout, suggests that the younger and smaller individual is responsible for determining the amount of play between the dyad. As in baboons then, relationships between individuals in chimpanzee social play is largely determined by age and size, with the smaller individual in a dyad taking the active role despite losing the "game". Alternatively, while any particular individual may lose play bouts against larger and older players, there will be some partners (i.e. younger and smaller individuals) against which he is able to win.

Thompson (1996, 1998) suggested a "self-assessment" function to play, providing immediate feedback for individuals on their physical abilities and competitive skills relative to their play partner's, which they could use to regulate future activities. She predicted that if well-matched play partners become mis-matched then a shift in preferred play partners should occur. Her theory rests on several assumptions, that play fighting should always be a dyadic affair, that it should occur at maximum intensity, and that players are not limited by choice of play partner; assumptions that are generally not met within the context of chimpanzee play. There is evidence in support of her theory in sable antelope (Thompson 1996) and some support from human studies on children (Humphreys & Smith 1984) and may describe a general function of play in species with stable social groups and immature peer groups. Related to this topic is the finding that wrestling among chimpanzee dyads was extremely fragmented. Biben (1986), for example, found that among immature squirrel monkeys, individuals, regardless of sex, preferred partners whom they could dominate during wrestling and with partners who they could not dominate, preferred dangle-play. These results suggest that for chimpanzees, the commonality of size asymmetry between play partners precludes a regular engagement in wrestling. Wrestling may only be useful if it provides valuable information on the relative strength of play partners and may be particularly relevant to similar sized play partners where this requires testing. When it doesn't, then individuals might shift to other games, which are less dependent on size and strength, such as dangle-play. While chimpanzee play mainly occurs between ill matched individuals and partner choice is constrained by both demography and by maternal associations, it is possible that if dependent offspring do play more with like-aged companions (Pusey 1990), when they

are available and engage in more wrestling or less fragmented wrestling, doing so, that self-assessment in this context could be an important function of play. Certainly, this is an area of research that deserves further study.

Some bouts appeared non-competitive in the sense that there was no definitive winner and loser. This could be interpreted as support for the existence of self-handicapping, whereby the larger individual restrains his own strength to that of his partner's, potentially allowing his partner to win occasionally. It was my feeling however that particularly within bouts involving very small infants, rather than self-handicapping himself, the older individual was restraining the younger, rather than competing directly with him. While the length of clear win/loss bouts appeared determined by the younger and smaller individual, in these bouts the roles appeared reversed, with the older and larger determining the length of the bout by manipulating the behaviour of the younger, possibly as a strategy for maintaining the interaction in order to ultimately strengthen the social bond between the pair. Possibly this is a strategy used by older offspring towards young infants as a way to "encourage" social interaction, since very young infants are least likely to win any games that they play in order to win or alternatively it could be a strategy used to assert dominance (see below). In other cases, such as when two offspring lay side by side and tickled or wrestled slowly, the game appeared non-competitive and to truly function as a way of maintaining positive social contact. In a sense, self-handicapping to a degree, is probably a common phenomenon exhibited by all older individuals in any ill matched play bout. Older individuals appeared to only exert themselves enough to take control of subsequent events or the behaviour of their play

partner; they certainly did not appear to exert their full strength. Certainly, Goodall (1986) acknowledged this when she wrote that actors must learnt to inhibit their aggressive behaviour and to curb their superior strength when playing with younger animals. This may be particularly relevant to males, who as adults perform stereotypical displays where aggression is inhibited and restrained to a degree.

4.4.2 Functions of Play: Social Cohesion and the Establishment of Dominance Relationships

As with human preschoolers' dominance interactions, the outcome of chimpanzee play interactions can be predicted on the relative developmental maturation of the participants (e.g. Savin-Williams 1979; Hawley & Little 1999). Winners and losers are on the most part easily identifiable and winning appears important. However, Boulton (1991, in Biben 1998) pointed out that competing to win is part of the competitiveness of play and is not to be considered competition for resources and Biben (1998) concluded that play is not a dominance interaction. Squirrel monkeys, which have a defined male and female dominance hierarchy from infancy upwards, do not improve their status during play interactions.

Results showed that rates of coercive behaviours were higher among male-male dyads than between female-female dyads and coercion in dyadic play, made up of male and female pairs, was more likely to be made by males. Rates of coercion among mixed dyads were closer to that of female-female dyads than male-male dyads, complementing dominance theory and sexual selection theory that predicts males will target other males

who are possible rivals for status. Human studies have shown that boys in male dyads attempt to gain leadership and dominance over one another more than girls in female dyads (Sgan and Pickert 1980 in Neppl and Murray 1997). Is coercion in play therefore an expression of one individual trying to dominate another?

As with human adolescents, R&T play becomes increasingly aggressive at adolescence (e.g. Pelligrini 1995). Neill (1976, in Pelligrini 2002) was the first to propose that human adolescents might be using it for the attainment of dominance status. Pelligrini (2002) proposed that R&T in humans might be involved in dominance in two age-related ways. The first is an indirect way, where individuals test and exhibit their physical strength (Pelligrini 2002) or, in other words, self-assess against their opponents. While the opportunity for self-assessment may occur infrequently among wild groups of chimpanzees, it may occur frequently among groups of similar aged individuals in captive groups. Paquette (1994) who studied the occurrence of play and aggression among four captive adolescents, who organised their relationships in a dominance hierarchy, explained the positive correlation between the frequency of play and the frequency of aggression outside of play, between dyads, as individuals using play to demonstrate strength and skills related to dominance. When challenges to the dominance order occurred at high frequency, play frequency between the pair was also correspondingly high and vice versa. However, increases in aggression also co-occurred with increases in gentle play and it is difficult to understand just how gentle play could function to demonstrate strength. Paquette's argument is further weakened by the fact that his observations could also be explained by the fact that play may have been used to

maintain harmonious relations and social cohesion between individuals, at a time when this may have been particularly important to reinforce. Pelligrini (2001) stated that stable relationships, such as friendships, support subsequent co-operation and inhibit aggression among group members. This suggests that play actually enhances cohesion among individuals of a group. I believe that within the play context offspring learn to form competitive relationships and learn prosocial strategies, such as co-operation, to attain goals or win, in ways that maintain harmonious relationships. In this sense, social play reflects the three basic tendencies governing interactions among primates: competition, social attraction and co-operation, integrated into a cohesive system of social relationships (de Waal 1987), which has both immediate and cumulative benefits.

The second way in which Pelligrini (2002) suggested that R&T might be involved in dominance is the direct assertion of dominance at adolescence. Learning just prosocial strategies to attaining goals provides opportunities for individuals to cheat and exploit the co-operative nature of play. Chimpanzee social play could escalate into aggression for a number of reasons. As for children aggression could be an "honest mistake" (Fagen 1981), such as one individual hitting or biting too hard. These events I termed "rough", since a vocal response by the victim was enough to terminate the "coercive" act and play resumed. Alternatively, chimpanzees, just like children, could exploit the playful tenor of play (R&T) in a more Machiavellian way, by turning play (R&T) into aggressive exploitation (Pelligrini 2002). While children may apologise for their mistake which was in fact intentional, chimpanzees sometimes continue being aggressive while giving a play signal, such as laughter, to mark their supposed playful intent. This is also referred to as

the "cheating hypothesis" (Fagen 1981), which occurs when one party turns play into aggression or a dominance display so as to extract some benefit, like dominance exhibition, over an unsuspecting play mate (Pelligrini 1995). Offspring learn that they can win by effective coercion toward younger individuals, without regard to peer evaluation and current or future social relationships (Hawley 1999). In other words, aggression may be seen as a form of "cheating", whereby the aggressor exploits the normally playful tenor of play (Pelligrini 2003). In some species, (e.g. punares Thompson 1998), the first aggressive act is normally performed by the losing individual suggesting that aggression may be used as a last resort to win. In chimpanzees, the individual most likely to win, i.e. the older and larger is more likely to be aggressive, and aggression is normally one sided, suggesting that in this species, aggression is not a necessary strategy to win and aggression is performed for other reasons.

In reality aggression is not commonly used before the adolescence in either chimpanzees or humans. However, even infant chimpanzees use aggression occasionally within play, towards their partner. While aggression is tolerated in chimpanzee society, the development of dominance relations, and as shown in chapter three, social relationships, are constrained and regulated by the mother's degree of sociability and her associations. Dominance relations probably do form in the short-term, i.e. for the length of time that the two individuals associate together. If an infant continues to charge and pilo-erect at her playmate, causing him to repeatedly retreat back to his mother, one can probably correctly conclude that a dominance relationship has formed. However dominance relationships among younger dependent offspring do not persist, mainly because mothers

regularly separate to range alone with their dependent offspring and because it is also probable that when the same two offspring meet up again, the "dominant" does not reaffirm this relationship. However, at adolescence dominance relationships appear to persist enough to become established to a degree, between certain dyads. Some offspring may consistently retreat from a late juvenile/early adolescent who tries to initiate play and it was my impression that one "aggressive" late juvenile/early adolescent male targeted and bullied only particular individuals. This suggests that though late juveniles/early adolescents are still constrained by their mother's behaviour, higher rates of aggression and reaffirmation of the outcome of previous dominance interactions may serve to cement their status. Rather than regard the development of dominance as being a characteristic of adolescence, these results suggest that play acts as a forum in which dominance behaviours can be practiced at an early age but which shift in importance during the age-span of the individual (Smith 1982, 1987; Boulton & Smith 1992; Pelligrini 1994, 2002; in Fry *in press*). These results therefore complement studies in human development that have shown that during adolescence boys' R&T play, functions to establish dominance status (e.g. Neill 1976 in Pelligrini 2002; Pelligrini 1995, Pelligrini 2003).

Studies of children support the notion that a dominance hierarchy exists much as it does in other primate groups (Savin-Williams 1979). However, most studies on human children have taken place in the school environment among stable social peer groups of like-aged individuals. In captive groups of immature chimps, who form permanent stable social units, dominance hierarchies do form (e.g. Paquette 1994) and dominance related

behaviours outside the play context occur to reduce intra-group aggression caused by competition over resources and to add stability and predictability to social relationships (Savin-Williams 1979). For their wild counterparts, the presence of a dominance hierarchy is highly questionable. Outside the play arena there are no observable winners and losers. A dominance hierarchy among dependent offspring does not appear to exist in the sense that dependent offspring do not appear to organise their power relations among all possible immature group members across contexts and behavioural settings. Competition and disputes normally arise within social play and to a lesser extent within the feeding context, possibly because play is the predominant context within which dependent offspring interact. If a hierarchy existed one would expect, after its establishment, aggression to be minimised rather than the observed increased rates from infancy to adolescence. This latter observation suggests that dominance status remains unresolved among immature chimpanzees, as it appears for some other primate species. Bernstein & Draper (1963) concluded in their study on rhesus macaques, that the occurrence of an unclear status hierarchy among juveniles was a product of both the developmental level and the ability of adults to effectively modify the response patterns of juveniles, by their presence. Biben (1998) showed that male infant squirrel monkeys, weighing 15-20% more than females, consistently demonstrated dominance over them and maintained a consistent and linear dominance hierarchy. Why juveniles of some primate species should maintain hierarchies, while others don't, is an interesting area of future research.

The results revealed that aggression occurs most frequently between dyads who were either unrelated, or who did not associate often together. While this suggests tangible benefits for mothers to socialise their offspring and for offspring to have a network of close kin, more importantly it suggests that aggressive individuals minimise the risk of alienation by victimising those who are least important to them. Pelligrini (2003) states that while agonistic strategies may be an effective way to initially establish status, continual use of these strategies in children is costly in terms of possible injury and alienation of conspecifics (Pelligrini 2003). Certainly young chimpanzees often appear wary of playing with early adolescent males, suggesting that the negative effect of aggression on other dependent offspring may also play a part in the reduction of social play frequencies in later adolescence. Pusey (1990) found that the percentage of time spent playing when potential play partners were present also dropped at adolescence, suggesting reluctance on the part of potential play partners to play or a drop in responsiveness of adolescents to potential play partners.

De Waal (1986, in Pelligrini 2001) also stated that conflict followed by reconciliation actually enhanced group cohesion. Results suggested that aggressors reconcile more often with their close relatives, probably reflecting the importance of these relationships to the aggressor, the motivation to maintain harmonious relationships with these individuals and an effective attempt to reduce the risk of estrangement.

As with humans, the co-occurrence of play and aggression at adolescence may serve to establish dominance relations. The fact that rates of aggression increase with age, that

juvenile and adolescent males more than females might spend more of their social time in R&T play and aggression occurs most frequently between males, suggest that the establishment of dominance relationships may be more important for males than females. Male adolescent chimpanzees (at a slightly older age than those in this study) start to disassociate themselves with their family groups to spend more time with adult males, in response to physiological changes at puberty. At this time adolescent males start to challenge adult females at increasing rates and accompanying this, at some point, is a decrease in social play frequency with other dependent offspring. In terms of causation, undoubtedly these behavioural changes, related to independence are in response to hormonal and maturational changes experienced at puberty, and social experience, including changes in the response of others to the individual (Pusey 1990), for both males and females. Aggression between dependent offspring occurs prior to aggression between adolescent males and adult females and both may provide a safe way to gain experience and practise that will be useful for males in entering the male dominance hierarchy, later in life. This switch from victimising dependent offspring to challenging females may therefore reflect a prior growing importance for male adolescents to use play in the establishment of dominance and to practise a range of related social skills.

4.4.3 Function of Play: Social Skills Hypothesis

While Pelligrini (2002) suggested that the social skills hypothesis gains the least support by offering no explanation for why there are sex differences in R&T (Fry, *in press*), among infant chimpanzees at least, there appear to be no sex differences in frequencies of social play. Aggression and agonism are an important consequence of social play among

immature chimpanzees; both occur more frequently within social play than in any other context. Rates of coercion and social play are significantly inter-correlated suggesting that play escalates into aggression and agonism. Rates significantly increased from infancy to early adolescence suggesting that play increasingly turns into aggression and agonism with age. Aggression can be viewed as one consequence of play and as results suggest, provides an opportunity for players and third parties to practice behaviour related to conflict resolution. Such behaviour, which is complex in chimpanzees, is far more likely to be learnt and require practice than aggression per se. De Waal (1987) illustrated this complexity by classifying adult aggressive interventions as, bond-dependent, scapegoating, breaking up fights, and exploitative coalitions. Observations suggest that offspring may be capable of breaking up fights, by approaching conflicts and initiating play with either the aggressor or the victim. Offspring may learn that interventions by third parties are dependent upon the degree of relatedness between the individuals involved and those present. The fact that coercion occurs at the highest rates between male dependent offspring, supports observations that social behaviours related to conflict resolution may be particularly relevant for males in rank acquisition, in later life. In effect, aggression in play allows all dependent offspring the opportunity to learn how to negotiate and develop social behaviours appropriate to adults of their sex (Pusey 1990) from an early age. Furthermore, as mentioned earlier, the restraint with which older individuals play with younger partners, in ill matched dyads, could be viewed as a skill in itself, since as adults, male displays, for example, are stereotyped and characterised by a high degree of restraint. Despite their impressive appearance, victims (myself included) generally escape with little injury (*personal communication*).

4.4.4 Differential Maternal Investment

Mothers appear to invest more into their infant daughters than infant sons, in terms of the frequency of support they gave them in agonistic interactions. This is an interesting finding because previous research had suggested that mothers might invest more in sons. Pusey (1978, in Pusey 1983) showed that sons groomed their mothers less than daughters in proportion to the amount that their mothers groomed them and mothers also supplanted their sons less than daughters at feeding sites. Pusey (1983) suggested that chimpanzee mothers at Gombe might invest in the sex with the greater variance in reproductive success, where reproductive success is less certain but potentially greater. The present result suggests that mothers might invest in the sexes in different ways and other studies suggest that sex-biased investment might be contingent on both the social rank of the mother and on which sex is philopatric and which disperses. In baboons, dominant mothers invest more in their female offspring, whose adult social rank they can contribute, whereas subdominant mothers invest more into male offspring because their eventual rank is less influenced by the mother's rank as they transfer between groups (Altmann & Altmann 1980, in Boesch & Boesch-Achermann 2000). Similarly, Boesch & Boesch-Achermann (2000) found that dominant chimpanzee mothers, at Tai Forest, Ivory Coast, invested about two more years in sons than daughters, while subdominant mothers invested more in daughters than in son, since daughters disperse at sexual maturity. Mothers are seen to support their sons actively in social life. An interesting prediction would therefore be that at Gombe, high-ranking mothers might support their infant daughters more in agonistic interactions than low-ranking mothers, if daughters of high-ranking females are more likely to remain in their natal community as adults and because

mother and adult daughter pairs form strong, enduring and supportive bonds. Differential maternal investment in daughters, in terms of affiliation and support, would suggest that mothers are using strategies that may, in the long-term, influence both the social status of their daughters and their tendency to disperse.

Because female infants learn they can count on maternal support, more often than male infants can, play may be the first context within which females learn the benefits of maternal support and intervention, which persisting into adulthood, may help both mother and daughter in rank acquisition. As chapter three shows, this bond is strengthened by the fact that female dependent offspring will play significantly more with female kin than male dependent offspring, suggesting that play, for female dependent offspring, allows females to develop social relationships appropriate to adults of their sex (Pusey 1990), which may be relevant to rank acquisition in later life. Mothers appear to support their male infants far less frequently, suggesting that support is not purely a maternal instinct to defend offspring. Although mothers do defend their adult sons in conflicts rank acquisition in adult males depends less on maternal affiliation and more on affiliative and opportunistic relationships with other males (de Waal 1987).

The support of victimised offspring by mothers corresponds to research showing that while adult males show a tendency to support aggressors in dyadic disputes, females show a tendency to support losers (de Waal 1984b in Smuts 1987). This sex-difference in the response to conflict among adults may therefore have its origin in the maternal

response to offspring victimisation. Female empathy may therefore derive from an adaptive maternal response.

5 Conclusions

5.1 Chapter Two: Female Dominance and Sociability

In chapter two I was able to show that dominance interactions between females occurred at much higher frequencies than those reported at some other field sites and the type of response was at least partially dependent upon both the context and the presence of adult relatives. Females could be ordered into a stable hierarchy, with age as a determinant of rank but results indicated a relatively high degree of non-linearity, probably due to the fission-fusion nature of chimpanzee society and the solitary nature of females.

High-ranking mothers and their adult daughters, who remained in the natal community as adults, consumed a greater proportion of energy rich foods in their diets and were more efficient feeders. Better nutrition may therefore account for high-ranking females achieving higher reproductive success (Pusey, Williams & Goodall 1997) and may explain why a large proportion of females at Gombe do not transfer as adults. These same females also spent more time in groups, suggesting that some aspects of sociability are determined by feeding efficiency. While females maximised their feeding efficiency by foraging alone, high-ranking females and their adult daughters appeared to be more able to afford associated costs of socialising.

Results also demonstrated that relationships between females were well defined, suggesting female relationships are an important aspect of chimpanzee society. The strongest social bond was between mothers and adult daughters but mothers also

associated at much higher rates with other mothers, than with childless females. This effect was probably due to the fact that similarly ranked and established females prefer to associate together, possibly as an adaptive strategy for effective coalition formation. These preferences were reflected in the grooming patterns, revealing a greater social attraction to and alliance with, kin over non-kin, adult female kin over adult male kin, high-ranking and established females over low-ranking ones and mothers over childless females, suggesting that grooming aids in the maintenance of coalitions (Seyfarth 1977, in Wrangham 1980). Mothers appeared to be able to control how much grooming they gave, but not how much grooming they received from other individuals. Younger females were able to spend a greater proportion of their grooming time grooming non-relatives than older females and the results suggested that the low frequency of grooming between females, compared to that between males, was due to constraints imposed on females by their offspring. As expected in a primate species with high within-group contest competition, differentiation of female-female association patterns, not apparent in the female-male association patterns, suggest that relationships among females may be extremely influential in the social structure of the community and the acquisition of rank may be more important to females at Gombe than for females in other populations.

5.2 Chapter Three: Offspring Sociability

In chapter three I investigated the long-term and indirect consequences of maternal rank and sociability on the social development of dependent offspring, since I reasoned that marked differences between Gombe mothers must affect certain aspects of their offspring's social lives. Results suggested that diet quality is an ecological determinant of

social play behaviour and supported the notion, as in other primate species, of a reduction in play frequency in response to a decline in resource availability (e.g. Biben 1998). Mothers who ate higher quality diets produced offspring who played more and offspring who ate higher quality diets also socially played more. Offspring of high-ranking females and their adult daughters, remaining in the natal community, socially played at higher rates, than the offspring of other females. In other words, those females who were able to secure high quality diets, and who could afford the costs of grouping, were not only more generally social, but they also produced offspring who were more social too, probably because both had more energy to expend in social activities and because these mothers brought their offspring into contact with the social environment more often. This was supported by findings that showed that mothers who spent more time in groups and spent a high proportion of their grooming budget, grooming females, produced offspring who socially played more; offspring whose mothers were closer in rank played more together and results that demonstrated that the frequency of social play between any two individuals was correlated to the degree of association between their mothers. This suggests that mothers determine the social milieu of their offspring and the offspring's social network mirrors that of its mother.

Results showed that offspring were attracted to play with individuals who they didn't associate with continuously and the number of players stimulated play duration, suggesting that dependent offspring might be encouraged to play by watching others play and supporting the notion that novelty in a new set of social partners and the motivation to investigate these "new" relationships may drive individuals to play. Since play

interactions are often the first interactions to occur between dependent offspring who meet after a period of absence, I argued that social play might serve a similar role in re-establishing relationships, maintaining familiarity, friendship (e.g. Pellis, Pellis & Mckenna 1993) and group cohesion, as social grooming has for adults. Since the social play rates of chimpanzees correspond with those of other non-human primates that live in permanent social groups and appears higher than those among captive chimpanzees, also living in permanent groups (Spijkerman 1986 in Brent *et al.* 1997), this suggests that wild living chimpanzees make extra use of social opportunities, to interact. I proposed that play may serve an indispensable function for young chimpanzees, living in a fission-fusion society, in social bonding and maintaining group cohesion. The social bonding theory is strengthened by the finding that dependent offspring play significantly more when the environment permits social bonding to be particularly effective, i.e. in both nursery and mixed groups.

Offspring appeared to form stable social play networks defined in terms of most frequent play partners. This selectivity was strongly related to kinship. Offspring played at higher frequencies with relatives than non-relatives and played at the highest frequencies with their sibling and their maternal kin, if their mothers were resident and well established. For offspring with no other adult maternal kin than their mothers, they played at the highest frequencies with non-relatives, whether or not a sibling was present and I proposed, since results suggested that offspring were able to maintain an optimal level of interaction within the constraints of their mothers' associations, that this might be an adaptive strategy by which such individuals "widen" their social network.

Female offspring played on average at greater frequencies with their female maternal kin than male offspring. Therefore, the strong attraction between adult female kin demonstrated in chapter two and thought to be an adaptive strategy for support in agonistic interactions, appears to be fostered from an early age. Play may therefore serve to promote relationships between kin that have significant fitness consequences in adult life, since female support is largely dependent upon existing social bonds. The fact that male dependent offspring did not play with male kin significantly more than female dependent offspring supports the notion that adult male coalitions are largely independent of previously existing social bonds (de Waal 1987) and maternal kinship. In this sense, play may be a forum in which immature individuals develop social relationships appropriate to adult of their sex (Pusey 1990).

5.3 Chapter Four: The Structure of Social Play Behaviour

In this chapter I sought to further investigate the nature and function of social play and in doing so provide more suggestions on its adaptive significance. Contrary to the definition of play as purposeless behaviour, I found that bouts were goal-directed and competitive. Chimpanzee social play could be classified according to the mutual goal of the players who competed for a superior position, for possession of an object, for possession of an individual (in the case of triadic bouts) or a combination of the above. Motor patterns were not random but appeared to be geared towards gaining physical advantage over an opponent and winners and losers were, for the most part, easily identifiable based upon postural differences and the winner's degree of control over subsequent events (Thompson 1998). These results were particularly striking, since I was extremely

sceptical of play's competitive nature, even after seven years of observation, until I analysed videoed play bouts individually.

Dyadic play bouts mainly occurred between ill matched partners, in terms of age and size, probably due to demographic constraints precluding peer groups of like-aged individuals. Since results from chapter three suggested that most frequent play partners were determined by maternal associations and kin relatedness, the theory that offspring might use play to self-assess their own physical performance, by playing with well-matched partners, seems an unlikely function. The older and larger individual won most play bouts while the smaller and younger one appeared to control the start and end of a bout, determining the amount of play between the two. This latter finding may reflect either restraint on the part of the older and stronger play partner, or a degree of attraction by the younger towards the physically superior partner. Winning appeared an important aspect of chimpanzee play, particularly for independently travelling infants, since these offspring spent more of their dyadic playtime playing with younger individuals, and results suggested that offspring of high-ranking females were more effective in maximising their probability of winning.

5.4 Chapter Four: The Functions of Social Play Behaviour

Results showed that aggression was an important consequence of social play and occurred more frequently between offspring within play than within any other context. A sex difference in the frequency with which mothers supported their male and female infants in conflicts, suggested that play may be the first context in which females learn

the benefits of maternal support, which, persisting into adulthood might help both mothers and adult daughters who do not permanently transfer to another community, in rank acquisition. Along with the findings in chapter three that female offspring play more on average with female kin than male kin, these results further support the theory that social play has an important role in social bonding and rank acquisition in later life. This was further supported by findings on sex differences in the rates of coercive and agonistic acts within the play context, which complemented dominance theory and sexual selection theory, predicting that males target other males who are possible rivals for status. I therefore proposed that coercion in play was a strategy used to assert dominance, increasing in frequency and importance with development so that by the time offspring, particularly males, had reached the late juvenile/early adolescent stage, dominance status had become established at the dyadic level, among some dyads at least. I doubted the presence of a dominance hierarchy however, since outside of the play context and across other behavioural settings, dependent offspring do not appear to order themselves in power relationships and the frequency of aggression within play increases with age, suggesting that dominance status among immature offspring remains unresolved. Results also suggested that aggression, as one consequence of play interactions, enabled offspring to experience both subdominant and dominant roles and learn important social skills related to conflict management and I proposed that the age and size asymmetry of dyadic play bouts, in general, enabled older individuals to learn restraint. The results therefore supported the "social bonding", and "complex social skills" functional hypotheses of play behaviour, which have both immediate and cumulative benefits, allowing individuals to learn how to negotiate their competitive relationships in a social setting from an early age

and also providing opportunities for dependent offspring to assert dominance. Results therefore suggest that play might have a crucial role in rank acquisition in later life, for both males and females.

The development of the drive to "win" apparent in social play, is best illustrated by a quote from Wrangham & Peterson (1997) who linked this drive to many aspects of a male chimpanzee's life but which could be applied to both sexes:

"The problem is that males are demonic at unconscious and irrational levels. The motivation of a male chimpanzee who challenges another's rank is not that he foresees more matings, or better food, or a longer life. Those rewards explain why sexual selection has favoured the desire for power, but the immediate reason he vies for status is simpler, deeper and less subject to the vagaries of context. It is simply to dominate his peers. Unconscious of the evolutionary rationale that placed this prideful goal in his temperament, he devises strategies to achieve it that can be complex, original and maybe conscious. In the same way, the motivation of male chimpanzees on a border patrol is not to gain land or win females. The temperamental goal is to intimidate the opposition, to beat them to a pulp, to erode their ability to challenge. Winning has become an end in itself."

5.5 Future Research

A detailed investigation into the distribution, availability, and seasonality of the food supply at Gombe and at other field sites, is necessary in order to understand how the social system of chimpanzees varies with the feeding ecology. Certainly, the longer we study chimpanzees from different populations, the more we appreciate just how varied these social systems are. However some differences may be more apparent than real: Are females at Gombe truly more aggressive because contest competition is more intense than at other field sites; or is the lack of evidence suggestive of female aggression, at other field sites, merely a bias on the part of researchers to following male only or mixed

parties, where female aggression appears to be suppressed? Being able to quantify the intensity of feeding competition between sites would help to answer question like these. Furthermore, being able to quantify the nutritional value of different foods would enable us to determine exactly the energy and nutrient uptake of different individuals and explain the variance in diet between individuals. For example, both the third- and fourth-ranking mothers in my sample, Gremlin and Sandy, spent smaller proportions of their feeding time feeding on fruit than any other mother, but ate greater proportions of termites. In the case of Sandy, termites constituted almost 40% of her time allocated to feeding during the study period. Since there was such a large variance in the proportion of feeding time allocated to termiting between different females, these findings led me to wonder whether some females who were less successful fruit competitors were able to counteract this by spending more time feeding on termites. However, this would only hold if both fruit and termites share some of the same common nutrients. This observation at least demonstrates that the variance among females to termite may have something to do with the variance in the quality of their overall diet. Being able to measure diet quality in a more precise way should be a goal of future research.

Just how grooming between females serves individual females throughout their life-spans, is also a topic of future research, especially since grooming patterns appear so varied among females at Gombe. Tanga, the lowest-ranking, youngest mother in the sample, who remained in her natal community with her alpha female mother, directed most of her grooming towards adult females. If grooming is traded for support and intervention, this suggests that Tanga is investing in a strategy that may help her to

acquire high rank. In contrast, Tita and Yolanda, two immigrant females, both also with just one infant each, spent most of their time grooming adult males. Tita, at least, received a lot of female aggression from resident females when she first arrived in the community, suggesting that immigrants may groom adult males in order to gain some protection from them against hostile resident females (either active defence or passive protection from being in close proximity). If grooming among females is an important tool in rank acquisition, this suggests that immigrants are at a disadvantage, since female aggression prohibits these females from forming bonds, in at least the short-term. This does not mean that immigrant females cannot attain high rank; Patti, the present alpha female, was also an immigrant, subject to female hostility when she first arrived in the community, who initially associated mainly with males. However, I suspect that it might take longer for immigrant females to attain status. A detailed comparison of the grooming patterns of both resident and immigrant females across their life spans might show how immigrants achieve integration and status within the female dominance hierarchy.

Following from this, a comparison of the life histories of offspring from both resident and immigrants would be an extremely interesting topic of research. While Tita appeared extremely motivated to associate and groom with adult males, her small infant, Tofiki, was the only infant who I observed adult males initiate play with. Adult males are not often observed to do this with infants, probably because mothers are extremely vigilant and protective of their infants in parties including males. However, Tita appeared especially popular as a grooming partner among males and therefore brought her infant son into close contact with them regularly, when males were present; her son appeared

especially confident in their presence. While such an apparently high level of contact with adult males might be detrimental to both mother and infant (Tita's son was killed by one male in the community in 2004, Pusey, *personal communication*) early experience associating with adult males might be especially important for male offspring and following the development of male offspring with differing levels of such experience might teach us something about the influence of males on development. This study focused on the influence of mothers on the development of offspring but if females show real differences in the extent to which they socialise with males, one would expect such differences also to affect aspects of offspring social development.

One topic of research, which had I the time, I should have liked to investigated concerns an aspect of mother-infant communication. Over the years I have noticed that if a mother is separated from her infant by a few metres (perhaps the mother is resting and her infant playing) and she decides to leave and travel away, she will sit up and conspicuously scratch her arm in long, slow strokes, while looking towards her infant. Often this is enough to get her infant's attention and her infant will approach, jump ventrally or dorsally and the mother will move away. Mothers at Mahale National Park apparently scrunch leaves on the ground (Gen Yamakoshi, *personal communication*), suggesting that this is culturally learnt communicative behaviour. In view of the growing literature on chimpanzee culture, I believe this very important to document. This behaviour is very subtle, and it is only because I have observed it in so many mothers that I am convinced that the scratch has a distinctive communicative function.

While my analysis sought to describe chimpanzee play in broad terms, I recognise that more could be gained from a finer-grained analysis of play bouts and comparative work among different primate species. Symons (1978, in Smith 1982) described the goal of play fighting in rhesus macaques as being able to bite without being bitten. This raises the question of whether of not this could also be a goal of chimpanzee play fighting.

Certainly play biting is a characteristic of dangle play and wrestling between chimpanzees. While it was my impression that play biting tickled the opponent, preventing effective manoeuvres that gave it an advantage, it wasn't my impression that biting was a goal in itself. However, descriptions of play are open to a degree of subjectivity; while I speculated that the goal of wrestling was to pin the opponent on the ground, wrestling bouts often lacked clear definition due to wrestling's fragmented nature. While I still adhere to the theory that dependent offspring wrestle to gain a superior position over the opponent, in much the same way that human children do, it is also possible that they simultaneously attempt to administer more play bites than they receive. If this is true, then almost certainly, older and larger play partners are more effective at doing this, in much the same way that they are more effective at winning in other respects, but it is an aspect of chimpanzee social play that deserves further investigation.

In chapter four, I suggested that play might function in the acquisition of rank, in later life. Confirmation of a long-term consequence of play, detectable later in ontogeny, would be extremely important in light of the fact that most functional hypotheses of play have traditionally concentrated on long-term benefits without providing satisfactory

evidence (see Martin & Caro 1985 for a review). One prediction, for instance, that could be derived from this study, is that animals that play more frequently as dependent offspring, are more successfully competitive as adults e.g. they acquire higher rank and/or are reproductively more successful. This is certainly a prediction that could be tested from years of long-term data that has been collected from Gombe.

Another area of potentially interesting research concerns why some juveniles of some primate species form dominance hierarchies, while others don't; how dominance hierarchies affect the nature of play and whether or not social play is a necessary prerequisite for hierarchy formation in juveniles. Immature baboons and vervets, in the wild, develop defined hierarchies (Lee 1983). Biben (1986, 1998) showed that in contrast to chimpanzees, captive squirrel monkey infants form consistent male and female hierarchies with male infants forming linear dominance hierarchies. All male infants are dominant to females and dominance is expressed across contexts. A proximate reason for this difference between these two species (assuming that wild immature squirrel monkeys also form dominance hierarchies) may be the fact that squirrel monkey male infants are 15-20% heavier than females, while no consistent difference exists between the sexes among chimpanzees. It is also possible that the more complex social skills related to conflict resolution in chimpanzees precludes the formation of hierarchies before the necessary skills have been learnt. In slow developing species, such as the Great Apes, the lengthy maturation phase to adult size, may allow the development of more complex hierarchies.

Biben (1986) showed that as a result of the presence of juvenile dominance hierarchies, squirrel monkeys preferred partners whom they could dominate during directional wrestling (wrestling) and with partners whom they could not dominate, they preferred nondirectional wrestling (dangle play), showing that dominance was a major influencing factor in the nature of play. Studying how hierarchies develop among juvenile primates will lead to a greater understanding of why some species do develop hierarchies and others don't and reveal whether social play is a pre-requisite for hierarchy formation.

Spijkerman et al. (1995) argued that the greater the variety of social partners in a rearing condition, the more individuals are able to develop social skills that will be advantageous to them in group life. Spijkerman et al. (1995) drew this conclusion from several studies that showed that chimpanzees reared in large social groups showed higher levels of dominance behaviours than chimpanzees reared in peer groups (Bloomsmith et al 1991, in Spijkerman et al. 1995) and rhesus monkey infants reared in a family showed higher levels of dominance and activity behaviours than infants reared only with their mothers and peers (Suomi 1974, in Spijkerman et al. 1995). In chapter Four I showed that dependent offspring, from high-ranking mothers, spent a greater proportion of their dyadic play time, playing with younger individuals and speculated that these offspring were more effective at maximising their probabilities of winning than the offspring of lower ranking females. This suggests that these offspring may be more competitive and develop superior social skills compared to other dependent offspring of the same age. A reason for this may be that since offspring of high-ranking females and their adult daughters play more frequently, they gain more experience and become more skilled in

competitive interactions. Related to this are aspects of the social rearing condition; chapter two showed that older females, who also tend to be higher ranking, have a greater number of dependent offspring than lower ranking and younger females and chapter three showed that siblings were often the most frequent play partners. Since mothers spend a large proportion of their time foraging solitarily, the presence and number of siblings may be instrumental in providing dependent offspring with effective opportunities to learn and practice social skills related to competition.

In the near future, the Kasekela community may be the last community to inhabit Gombe National Park. This won't necessarily mean the end of the chimpanzee population. The community could expand in number, as it has been doing presently by absorbing stranger females, expand its territory, thus acquiring more food sources, and experience an overall increased reproductive success. Groups could become more stable and party stability could produce female power (Wrangham & Peterson 1997). Following how relationships change in the face of ecological and social changes may mark a very exciting time for chimpanzee research and contribute to a greater understanding of the interaction between primate ecology and social relationships. Party stability and female power could mark a change towards a more (between the sexes) egalitarian and pygmy chimpanzee-like society, as it has been described at Tai Forest, Ivory Coast (Boesch & Boesch-Achermann 2000) especially if increased food availability could afford females a greater number of sexual cycles and concealed ovulation (see Wrangham 2002). Female philopatry, very possibly a response to the changing fates of the two neighbouring communities, has resulted in some very strong social bonds between some females.

Possibly female philopatry has increased the pressure for resources and helped define the female dominance hierarchy. Fifi, for instance, was the only female who was consistently observed in a party of males, successfully begging for meat and if her adult sons had possession, she appeared to have no qualms in snatching a large proportion of it, in front of other adult males. Fifi was also the only female I observed displaying unprovoked in front of unrelated females, with or without the support of her adult kin. Fifi was not only the most reproductively successful female observed at Gombe (and possibly across all other field sites), she was also the most powerful and influential female in the community, and this power did not diminish when she lost her alpha position. Certainly, as chapter three demonstrated, such changes will shape the social lives of the offspring and monitoring intra-community social relationships in light of these ecological and social changes should be an important aspect of future research.

5.6 Conserving Gombe's Chimpanzees

Ironically, it wasn't until I had spent some time at Gombe that I really appreciated just how endangered chimpanzees are. Ironic because Gombe is supposed to be a protected environment where chimpanzees are safe. When I first arrived at Gombe, the northern Mitumba community had just suffered a pneumonia epidemic that had drastically killed a large proportion of the group, including half of the adult males. After that, pneumonia epidemics that chimpanzees showed little resistance too became a regular feature of Gombe life. Over the seven years that I worked at Gombe, there were at least three separate pneumonia epidemics and one severe scabies outbreak, all of which claimed lives. However, epidemics have long-term and far-reaching consequences for the

surviving chimpanzees and for the chimpanzees of neighbouring communities, altering group dynamics and inter-group interactions. After the epidemic in the Mitumba community in 1996, the community was left with just three adult males, in effect, leaving the community extremely susceptible to raids from the Kasekela males. In subsequent years the Kasekela males were able to expand their territory northwards, until by the time I left, during the first half of 2003, the Mitumba chimpanzee community was confined to just the most northern valley in the Park.

In 1999 I started surveying the southern-most and only unhabituated chimpanzee community in the Park, the Kalande community. From the early 1990's there were indicators that this community had suffered a dramatic decrease in numbers. The Kasekela community had over the years expanded their territory range significantly south, and sightings and calls from the Kalande community had become increasingly rare. By 2000 we were confident enough to estimate that the group had fallen to between 15 and 25 individuals (from an estimated 50 during the 1970s and 1980s) but the cause of the decline was harder to determine. Certainly snaring and hunting of fauna occurred, on two occasions I heard automatic gunfire in the southern valleys and the Kalande community's range remained extremely poorly protected. It wasn't until the end of 2002 that we found a possible answer. During September of that year the Kasekela community contracted a cold. Luckily it didn't develop into pneumonia, and all individuals made a full recovery. However, a month later, researchers studying the Kalande community observed chimpanzees there with identical symptoms that quickly developed into pneumonia. Three bodies were eventually recovered but these chimpanzees were not

habituated and there remained a real possibility that many others had died. Over the following year, which included a fruit season, which in previous years had resulted in many sightings by researchers, observations of chimpanzees decreased dramatically suggesting that a significant decline had occurred. As a consequence of the decrease, 2003 was marked by the arrival of a comparatively large number of stranger females into the Kasekela community, suggesting that numbers of males had dropped so low, remaining females had been forced to transfer. The relatively short time between the sicknesses in both the Kasekela and Kalande communities suggested that the Kasekela chimpanzees had transferred the virus to the Kalande community, possibly via peripheral females ranging between the two groups. Presently the largest group sighted in the south of the Park is seven, compared to 14 in 2000.

For long-term researchers, like me, death and the fear of another epidemic was something we lived with at Gombe. Each year it seemed that chimps were dying or disappearing and if they didn't, we began to wonder when they would. The death of the adolescent male Galahad was a defining moment for some of us, since Galahad was everybody's favourite chimpanzee; we all had high expectations for an individual who had such an animated and ambitious personality. None of us ever expected that his life would be cut short, so soon. Because the chimpanzees showed so little resistance to these pathogens and can contract the same diseases as human beings, we all drew the same conclusion that the epidemics were human induced, although the possibility remains that their susceptibility to disease is a product of inbreeding caused by the population's increasing isolation over the last century, or a combination of the above: a greater susceptibility to human diseases

caused by increasing isolation of this small population. Presently Gombe is a small island surrounded by a dense population of villagers and within the Park, a dense population of researchers, and National Park personnel. The chimpanzees regularly foraged within the area designated for human settlement, they were regularly hand fed bananas making them extremely habituated to the presence of people, rules and regulations governing the distance with which tourists and researchers were allowed to approach the chimpanzees, regularly not enforced, rules forbidding sick tourists and researchers into the Park, regularly not enforced and villagers regularly walked on public trails between the villages into the Park. In The Shadow of Man, Jane Goodall describes a polio epidemic that the Kasekela chimpanzees contracted during the 1960s. At the same time polio was affecting many villagers living around the periphery of the Park. Clearly (it appeared to us) humans had been the vectors of this disease. Ironically those people who care most about protecting the chimpanzee population at Gombe, the researchers, the Park personnel and the tourists, are most likely the source of one of the main causes of the systematic decrease in numbers over the years. To put the numbers in perspective, Jane Goodall estimated the Gombe population in 1986 to be about 160 individuals. Presently the number has halved.

Thanks to Jane Goodall the Park exists and the population remains in existence. Undoubtedly without research and the establishment of a national park, the forest would have vanished decades ago, but we should now question whether chimpanzees and in fact all Great Apes are suitable subjects for (intense) habituation and subsequent research and

tourism. Despite the fact that there are no alternative ways to conserve such animals, I don't believe that they are.

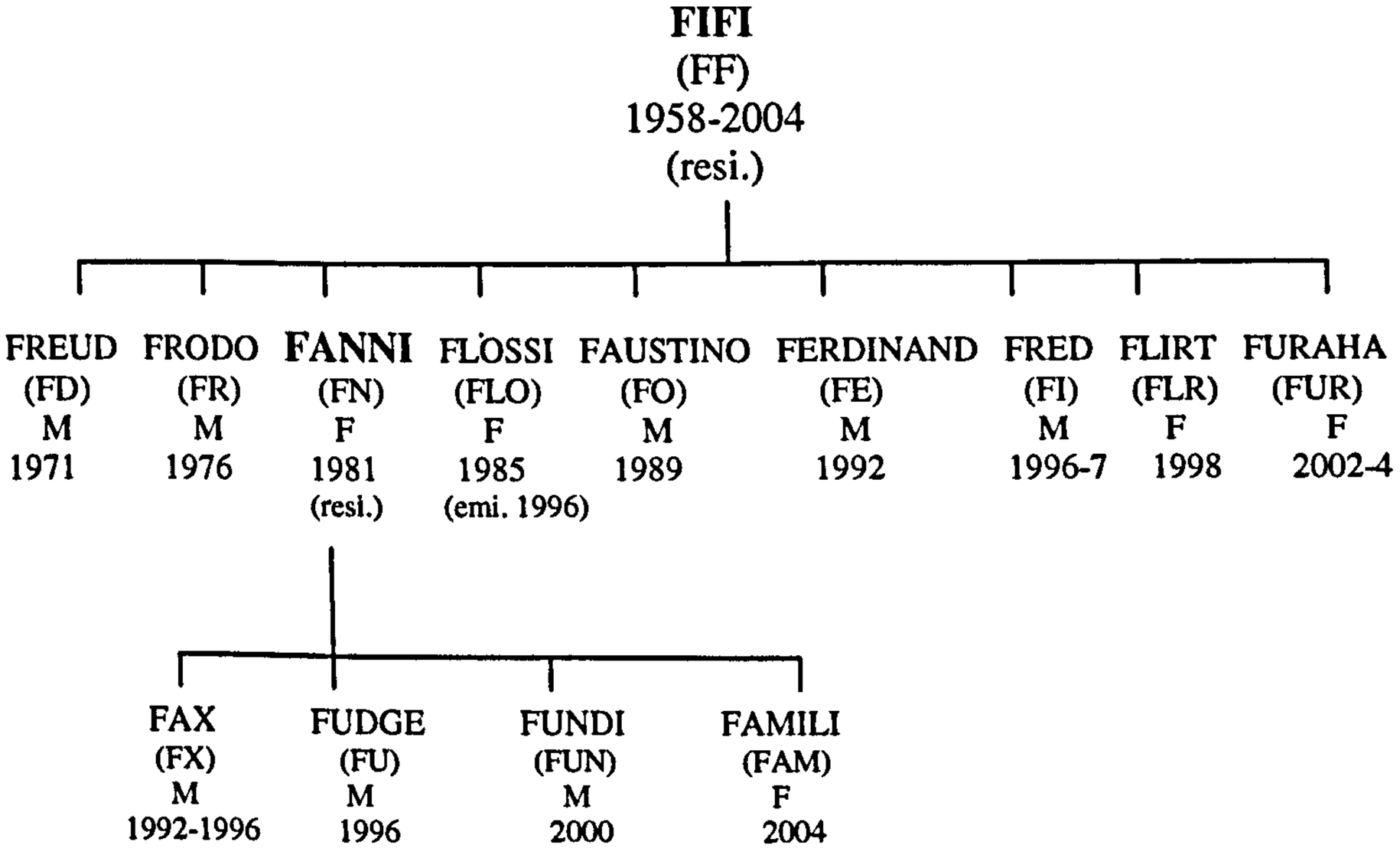
As Jared Diamond argued in the Rise and Fall of the Third Chimpanzee (1991), on the basis that both human and chimpanzee ancestors diverged somewhere between five and eight million years ago and both share 98.4% of their genetic material, humans do not, by the rules of cladistics, constitute either a distinct family of a distinct genus. Following zoological classification, since *homo* was proposed first, it takes priority over the name *Pan* (Diamond 1991). In effect there are three species belonging to the genus *homo*, humans, chimpanzees and the pygmy chimpanzee.

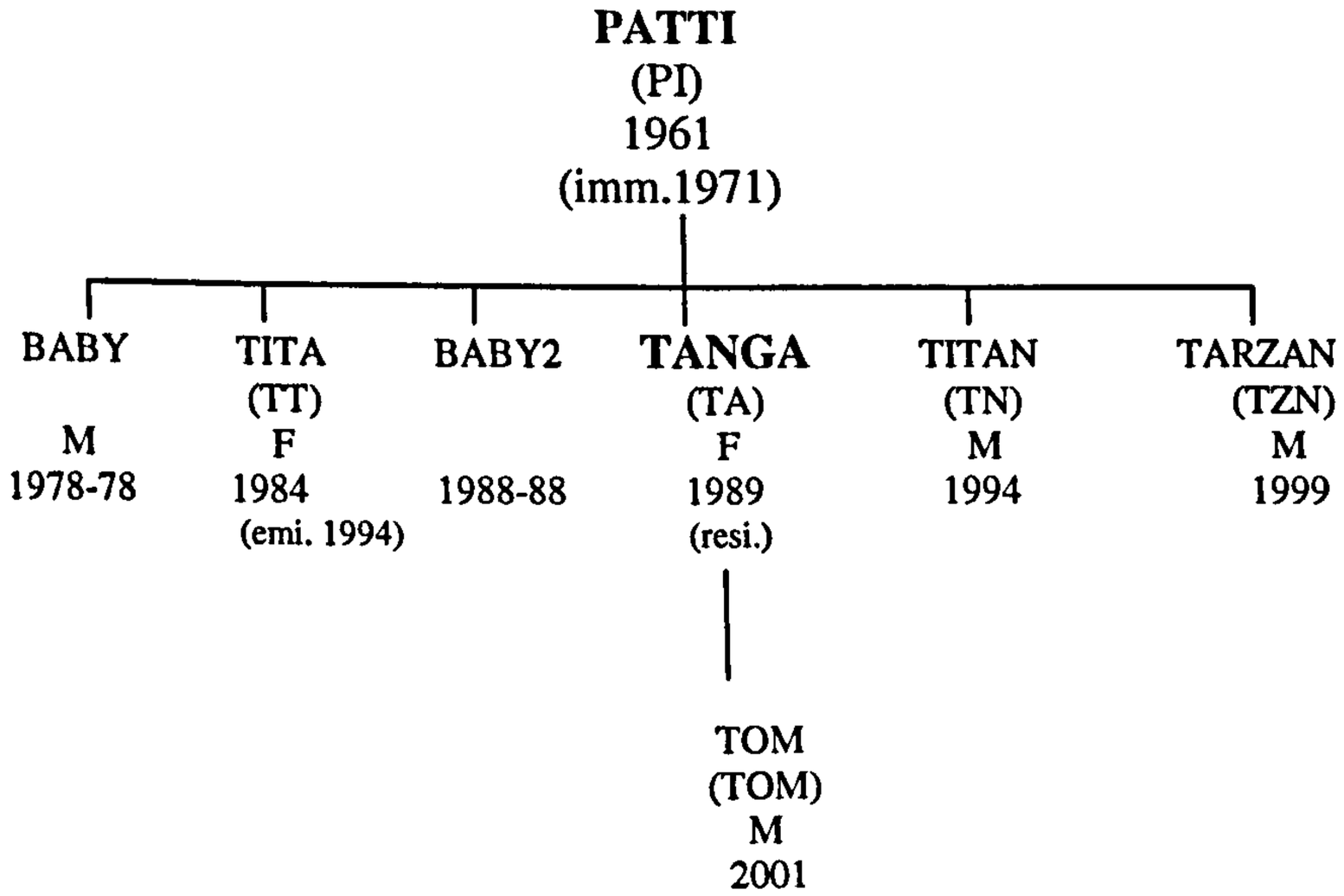
The fate of the chimpanzee appears to be following the same course taken by low density people with less advanced technology, in the face of invasions by numerous, technologically advanced people; a fate that has repeatedly occurred in our modern world. When North and South America were invaded by Europeans, indigenous people succumbed to introduced epidemics, while survivors were killed outright or driven off their land (Diamond 1991) a pattern almost identical to that continually occurring in and around Gombe. Like the chimpanzee, indigenous people were regarded as sub-human and this attitude repeatedly prevails today in areas where ethnic conflict progresses to genocide. Likewise, prehistorically, the arrival of humans in areas of the world previously uninhabited repeatedly coincided with mass extinction of other species and more recently, the downfall of pre-industrial civilisations which gave birth to such innovative and long-standing developments such as agriculture, animal domestication and writing, have been attributed to the destruction of natural resources. While the argument

holds that apes should be given stricter ethical consideration, our own history of the way we treat our own species and our natural resource base makes doubtful that this will ever occur.

APPENDIX 1:
FAMILY TREES OF MOTHERS SAMPLED

Key: full name; abbreviated name in brackets; year of birth and year of death where appropriate; M = male; F = female; emi. = year of emigration; resi. = resident female; immi. = year of immigration into community.





GREMLIN
(GM)
1970
(resi.)

GETTY	BABY	GALGAHAD	GAIA	GOLDEN&GLITTER		GIMLI
(GT)		(GD)	(GA)	(GLD)	(GLT)	(GIM)
M	M	M	F	F	F	M
1982-86	1987-87	1988-2000	1993	1998	1998	2004

SANDY
(SA)
1973
(resi.)

SHEREHE	SAMSON	SAMANTHA
(SR)	(SM)	(SAM)
F	M	F
1991	1996	2001

INFANT
2004

TREZIA
(TZ)
F
1978
(immi. 1991)

ZEUS	ZELLA
(ZS)	(ZLA)
M	F
1995	1999

TITA (misnamed, not Patti's daughter)
(TT)
?
(immi. 1996)

TOFIKI
(TOF)
M
(2000-2004)

YOLANDA
(YOL)
1986
(immi. 1996)

YAMAHA
(YAM)
F
1998

Appendix 2:
Ambiguity in Female Relationships

Here I illustrate the non-transitive nature of the female hierarchy with some observations on the nature of the relationships between the three highest-ranking females, Patti (the alpha), Fifi and Gremlin (second and third in rank, respectively). In some respects all three females can be considered friends, as defined by Boesch & Boesch-Achermann (2000), in that they share similar ranges, interact peacefully together and their offspring often play together. Although aggressive interactions between mothers, in the support of offspring, have often been considered uninformative in terms of dominance relations, since it is believed that even low-ranking females will support their young against higher-ranking females, I do not support this view. For example, I have observed instances where a mother reacted with submissive gestures in response to her juvenile offspring being chastised by another higher-ranking female. The following observations serve to illustrate this point and to show the complexity of female relationships, in part, as a function of their offspring's behaviour.

Patti's late juvenile/early adolescent son Titan was often aggressive, "bullying" infants, including his infant sibling, during play. When both Patti and Gremlin associated together, Titan often focused his aggression on Gremlin's infant twin daughters. This invariably led to Gremlin punishing Titan, despite Patti being higher-ranking. During one particular afternoon, Titan repeatedly attacked Gremlin's infants and Gremlin responded by mildly threatening Titan on each of these occasions before the group eventually nested together for the night. The following morning, without any provocation, Gremlin

descended from her nest, walked straight over to Titan and viciously bit him on the back of the neck, starting a fight between the two of them. Patti, who was at this time still in her nest, hurriedly descended, watching both Titan and Gremlin and vocalising, but she did not actively defend Titan against Gremlin.

In contrast the effect that Titan's aggression had on Fifi was the direct opposite of its effect on Gremlin. Historically, up until 1997, Fifi was the highest- ranking female and had always been an extremely aggressive female (see Goodall 1986) and on at least two occasions was observed to try and kill newborn infants (see below). During 1997, the community suffered from a severe scabies epidemic. Fifi became very ill (and her infant son died) and during this period Patti became the highest-ranking female, indicated by a reversal in pant grunting between the two of them. The mechanism by which this occurred is unclear but it may have been similar to that frequently observed between males. Very often, at Gombe, an alpha male is challenged during a period of ill health (personal observation) and while following Patti during this period I observed the only challenge on Fifi's status by Patti. Patti, who was alone at the time, suddenly charged, hair erect, into the undergrowth where Fifi was quietly sitting. Fifi responded by pant-grunting to Patti. The charge appeared unprovoked and could only be understood within the context of a challenge of power or the alpha position. In contrast to Fifi, Patti, despite her large size, was not a particularly aggressive or social female and had no female adult kin in the community at that time, which made the interaction even more surprising. Soon after this, Fifi was observed to pant-grunt to Patti, and on at least one occasion I observed

Fifi avoiding Patti feeding in a tree, which she appeared to want to feed in (having travelled directly over to the tree while foraging).

During the data collection period of this study (2001-2003) I never observed Fifi to defend her infant/ early juvenile daughter, Flirt, from Titan's aggression, in Patti's presence. Even when Titan relentlessly provoked the situation, Fifi would only vocalise in response. During one particular day at the start of March 2003, Fifi and Flirt met up with Patti and her sons, Titan and infant Tarzan. Titan immediately descended a tree bristling with a small mammal carcass in his mouth. Fifi and Flirt peered at the carcass and then Titan left to climb a tree and feed. Flirt followed Titan to peer at him while he fed on the meat. Twice he attacked her and Fifi, lying ten metres away, mildly grunted in response. When Patti moved away Titan and Tarzan followed and after some minutes Fifi and Flirt approached. As Fifi approached, Titan climbed down from a tree and rapidly approached, which elicited pant-grunts from Fifi. Titan presented his back to Fifi and she continued to pant-grunt, while bobbing her head into his back. This behaviour was extremely surprising. Titan hadn't reached an age to start seriously challenging the lowest-ranking females, let alone the second highest-ranking and possibly the most aggressive female in the community, but it may illustrate the influence that the presence of the alpha female can have on her offspring over other individuals.

That evening, Fifi, Patti and their offspring nested close to each other, although the following morning Titan, Fifi and Flirt were observed without Patti and Tarzan. Titan stayed with Fifi that day, which is unusual behaviour; offspring rarely leave their own

family groups to associate with another, especially one with which they are maternally unrelated to. On two occasions Fifi threatened Titan with her hand, flicking her wrist in his direction, and on a third occasion she threw a rock at him. Titan responded by running off but maintained close enough proximity to nest with her that night. The following morning, while feeding, Fifi threatened Titan again and a little later Patti arrived with Tarzan and another female Skosha. Fifi approached Patti and pant grunted to her. Titan also approached and began to groom Patti, while Fifi continued pant grunting to Patti. Titan then jumped around Patti, approached Fifi and, while standing bipedal, made pelvic thrusting movements into Fifi's face as Fifi continued to pant grunt to Patti. Only later in the day when Tubi, an adult male, was present did Fifi, with support from Tubi, display at Titan in response to an attack on her daughter Flirt.

These anecdotes highlight two things. First female relationships are complex and because interactions between females are rare compared to those between males, difficult to understand. Quite possibly Patti's challenge on Fifi' alpha status had a psychological impact on Fifi, comparable to that of an alpha male losing his status. It remains, for instance, difficult to understand why having lost alpha status, a male never appears interested in regaining that status even when the opportunity arises (personal observation), although males may chose less stressful strategies (see Muller & Wrangham 2004), such as coalitionary support of the alpha, and reap some benefits through the alpha's dependency on the relationship (Nishida & Hirai-Hasegawa 1987). Long-term consequences of defeats have been recorded among males in the Tai population of chimpanzees where the former alpha, Brutus, who was defeated by Fitz, pant-grunted

least to the alpha male (Boesch & Boesch-Achermann 2000). The fact that females are partially solitary, and as a consequence interactions occur rarely, may result in defeats having longer-lasting effects on females. Fifi appeared the only female to act in such a submissive fashion towards Patti. Although other females were observed to pant grunt to Patti, all females pant grunted to Fifi. If Patti was the highest-ranking female, then Fifi was certainly the most powerful, displaying through groups of females unprovoked, with or without the support of numerous adult kin. From an observer's subjective standpoint, all females except Patti appeared to regard Fifi as the highest-ranking female perhaps because she had been an aggressive alpha female for so long and had many adult offspring in the community who she could rely on to give her support.

Second, these anecdotes show that the way females interact with the offspring of other females illustrate underlying relationships between females. Gremlin may have been able to retaliate against Titan because, just like males, Patti may have depended on her alliance with Gremlin, while their relationship had never been challenged and had always remained amicable. Furthermore, in considering the behaviour of Titan, just like baboons (Altmann 2001), these anecdotes indicate the possibility that offspring can monitor and respond to the relationships between females. My impression from the seven years I studied chimpanzees at Gombe, over the course of Titan's development from infancy to early adolescence, was that Patti's association with Fifi and Gremlin gradually decreased, suggesting that this may have been in response to Titan's increasingly aggressive nature. While she may have relied on Gremlin's friendship for support in certain contexts, she may have been forced to associate less with her, in order to maintain this relationship.

I cannot write this section without trying to make sense of Fifi's infanticide attempts on Gremlin's newborn infants. Goodall (1971) first described the phenomena of female infanticide, when over a course of years, the highest-ranking female at that time, Passion, and her adult daughter, Pom, were observed to hunt down, kill and partially consume, a number of new-born infants in the community. Many other unexplained disappearances of infants at this time were speculated to be caused by Passion and Pom's infanticidal tendencies.

In 1991, Fifi, the second highest-ranking female, at that time, was observed, along with the highest-ranking female, Gigi, to attempt to hunt and attack Gremlin's newborn infant, Gaia. In 1997, in coalition with her adult daughter, Fanni, Fifi again attempted, unsuccessfully, to hunt and kill Gremlin's new-born twins, on the same day that Gremlin returned to the group, after their birth. At about this time several other new-borns unexplainably disappeared.

Infanticide ha been documented in many animal species. In species such as gorillas *Gorilla gorilla* and lions *Panthera leo*, infanticide poses a formidable risk to females and shapes the very core of their society (Wrangham & Peterson 1997). During a group take-over, males will often kill the infants of the females present. Subsequently, the females resume their sexual cycle faster, are attracted to mate with the killers and males are assured paternity of subsequent offspring without having to take care of offspring fathered by unrelated males. The killer's genetic interests are served by infanticide because he removes the competitor's genes (Wrangham & Peterson 1997). Male

chimpanzees, likewise, have been observed to kill the offspring of stranger females they encounter on raids into the territories of neighbouring communities. Wrangham (1997) argued that two species-typical behavioural conditions, party-gangs and bonded males, were sufficient to account for the tendency of chimpanzees to look for killing opportunities when hostile neighbours meet because killing under these conditions is cheap and will pay, at least by reducing inter-community competition for food resources. Williams *et al.* (2004) also showed that males defend a feeding territory for themselves and the resident females of their community and use strategies in an attempt to remove feeding competitors, with infanticide viewed as the removal of future competition. However the phenomenon of female infanticide, occurring within a community, is by far the hardest to explain in terms of its adaptive significance.

Female infanticide appears to be a phenomenon of the alpha female, in coalition with another female ally. Alpha females along with their adult daughters appear to be the most common pattern at Gombe, probably because the bond between females and their adult daughters, who don't transfer, is the strongest kind. The fact that a female forms a coalition with another female before attempting infanticide is not in itself surprising, since it undoubtedly increases the chance of success. Furthermore, victims of female infanticide are always new-born infants. Infanticidal females have never been observed to attempt to kill older infants, as if observing the new-born for the first time, or the pungent meaty smell of the mother after birth, is in itself enough of a stimulus to elicit an infanticidal response.

My own interest in this topic stems from the fact that I witnessed Fifi and Fanni's infanticidal attempt on Gremlin's new-born twins in 1997. This incident will forever stand out as one of the most horrific events that I had to force myself to watch as an objective spectator. Three questions arose from watching this. First, why do females attempt to kill new-born infants of other community females? Second, why did Fifi attempt to kill the new-born infants of her a close friend Gremlin? Third, why did Gremlin resume her normal and relatively high level of association with Fifi, just a few days after Fifi attempted to kill her offspring? While I can only speculate on the first two questions, i.e. it is an extreme expression of dominance and power by the alpha female; it may serve to reduce competition for resources in an environment where females have to compete intensely; it may enable the alpha female to increase her core area, sufficiently to accommodate her adult daughter (Pusey 1983), I can, with the knowledge gained from the research I have done on female relationships, theorise on the third. What my research shows is that female relationships and support between females is an extremely important component of chimpanzee society and probably has a direct effect on the reproductive success of individual females. High-ranking females are reproductively more successful and produce female offspring who, if they don't transfer, eventually gain high-rank, in part through the support of high-ranking kin, particularly mothers. Gremlin as a high-ranking female has no adult female kin in the community (although her daughter Gaia is presently reaching adulthood). Her closest associations, at the time of this study, were with Fifi, Patti and Fanni who she formed coalitions with against the aggression of males, even that of her adult brother and also against peripheral, stranger females. Therefore, in light of this, it was probably even more important for her to maintain these associations,

despite the fact that some of her closest associates had turned temporarily against her. If she had had adult female kin present, then it is possible that she would have expressed a greater reluctance to have continued her close association with Fifi and Fanni or perhaps her associations with Fifi and Fanni wouldn't have been that close to begin with. What this incident perhaps demonstrates is that females who don't have close adult female kin in their community, despite having close associates with non-kin are, at certain times and in certain situations, vulnerable to extreme forms of female aggression that have a direct impact on their reproductive success. It will be particularly interesting to see how Gremlin's associations change over the next few years as her daughter reaches adulthood and assuming her daughter decides to stay in her natal community. It has always been my impression that the changing age of offspring impacts a mother's female association patterns. Particularly because interactions between females occur at such low rates, compared to interactions between males, it is imperative that long-term studies continue in order to understand female relationships fully.

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